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Chas Macklin

Skull

The Skull of a Human Fetus of 40 mm.

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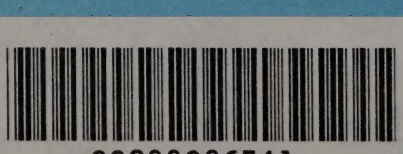
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THE SKULL OF A HUMAN FETUS OF 40 MM.

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INTRODUCTION

Researches upon the developing human skull have been carried on by various investigators, for a summary of whose results reference may be made to the excellent reviews by Jacoby ('94) and Levi ('00). The plate method of reconstruction, however, has been applied in such investigations only within recent years, and has been used in the study of fetuses in the following stages:

LENGTH	PROBABLE AGE (AUTHOR'S ESTIMATE)	AUTHOR
mm.		
13		Levi
14	37–38 days	Levi
17	42–45 days	Levi
17	50 days	v. Noorden
18.5	7½ weeks	v. Noorden
23	8½ weeks	v. Noorden
30		Jacoby (younger than the 28 mm. stage of Levi)
28	58–62 days	Levi
30		Fawcett
80		Hertwig

It will be seen that a considerable interval occurs between the last two stages in this list, and with a view towards lessening it I undertook, at the suggestion of Professor McMurrich, the study of the skull of a fetus of 40 mm., crown-rump measurement, which would correspond, according to Mall's formula (Mall '06, p. 439), to an age of 63 days. The entire head of the fetus had been cut into serial sections in the frontal plane, the sections being 20 micra in thickness and stained with haemalum followed by erythrosin. From these sections the entire skull, together with the membrane bones and upper two visceral arches, was reconstructed by the wax plate method at an enlargement of 30 diameters, and, to facilitate the study of the nasal and otic capsules, separate models were made, at the same magnification, of the mesethmoid, ectethmoid, right otic capsule and the anlage of the right osseous labyrinth. Drawings were made of every other section by the use of Edinger's "Drawing and projection apparatus," only that tissue being included as cartilage which presented a homogeneous, blue ground-substance and could be clearly differentiated from its surroundings, i.e., the tissue which Levi ('00) has described under the terms 'alteren Vorknorpel' or older precartilage, and "Knorpel" or cartilage. The earlier chondrogenic tissue of which there was very little at this stage, was disregarded.

The sections were not exactly in the frontal plane and to eliminate any lateral distortion in the models the amount of obliq-

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uity was determined as accurately as possible and the wax plates piled upon a plane adjusted at the proper inclination. It is also to be noted that a few sections passing through the dorsal extremity of the occiput were wanting from the series, and the small portion of the occipital region which they represented has been reconstructed by reference to other models, the parts so added being painted white, so that they may readily be recognized.

In the following description of the models I have used, as far as possible, the terms which are current in the literature, and when those referring to the human skull were exhausted recourse was had to the terminology in use in the more recent publications upon the chondrocrania of mammals. Preference is given to the BNA, and names not hitherto introduced into human chondrocraniology are usually followed by the name of the author who has employed them, the ideal being always kept in view of a system of terms uniform throughout the mammalian forms at least. New names, introduced by the writer, are indicated by making their initial appearance in italics.

An attempt has been made to select such terms of orientation as may be applied to animals having either a horizontal or a vertical long axis. Thus the terms ventral, dorsal, cranial, caudal, lateral and medial are generally used, but their respective equivalents for the human figure, such as anterior or front, posterior or back, superior or upper, inferior or lower, external or outer, internal or inner, are also employed. Oblique directions are indicated by combinations of the above terms.

Measurements appearing in the text have been taken from the models, and are thus magnified thirty times.

THE SKULL AS A WHOLE

The primitive skull of homo at the 40 mm. stage presents, in general, the characters which have become familiar through the illustrations and descriptions of v. Noorden, Jacoby and Levi for younger embryos, and the model of Hertwig for a more advanced age, combined with several features that are characteristic of this period of development. The outline, when the many gaps are filled in, suggests the osseous skull.

Viewed from above (fig. 1) we note the entire absence of the roof and the extremely rudimentary character of the sides of the cranial vault. The eye meets with an irregular surface of varying depth, surrounded by a broken, ovoid contour, the smaller end being ventral. This surface we recognize as the floor of the primitive brain-case. Its dorsal half is made up of the future posterior cranial fossa, a deep, bowl-like enclosure, the steep sides of which slope rapidly down to an elongated opening in the floor—the primitive foramen magnum. In the ventral wall of this fossa is a trough-like space behind the basilar plate, flanked by two rounded eminences, the partes cochleares of the otic capsule, and terminated above by the horned, ridge-like dorsum sellae, which forms a conspicuous object in the floor of the cranium. Passing forward over this ridge a sideless pit, the hypophyseal fossa, comes into view, which marks the center of the middle cranial fossa, and here, in the region of the body of the sphenoid, the cartilaginous floor is very narrow. Lateral to the corpus sphenoidale is a large, triangular gap in the floor and sidewall of the brain-box, the apex of which meets the side of the sella, while the ventral and dorsal borders are formed by the dorsal border of the ala orbitalis and the cranio-ventral surface of the otic capsule respectively. Forming a lateral, knobbed projection beneath the ala orbitalis is the relatively small ala temporalis, and this is observed to lie ventro-caudal to the plane of the above-mentioned triangular space, just as, in the osseous skull, the greater wing lies below and in front of the plane joining the lesser wing with the petrous portion of the temporal bone. As will be seen later, this plane corresponds in a general way to the situation of a primitive floor and side-wall of this region of the skull, as found in the lizards. Two of the bones which will later wall in this space, viz., the parietal and the squamo-temporalis, are as yet very rudimentary, while the third, or ala temporalis, has only just commenced to ossify.

We now pass forward, over the low ridge in front of the sella turcica, known as the tuberculum sellae, and come upon the plateau-like surface supporting the optic chiasma, which leads laterally into the optic foramina. Ventral to this surface is the

wide, upward-slanting, anterior root of the ala orbitalis, in front of which is a broad, flattened, triangular surface. This we recognize as the floor of the anterior cranial fossa. Perforating it, in the area lateral to the median septum, which represents the developing cribriform plate, are several foramina, the largest being the paired fenestrae cribrosae. Hook-like, backwardly projecting processes mark the dorso-lateral limits of the floor, which ventro-laterally is widened by the orbital plate of the frontal bone.

The only portions of the osseous cranial vault yet in evidence are the rudimentary frontal portion of the frontal bone and the net-like parietal—these being separated by a rather wide space.

Finally, the cranial aspect discloses to view certain accessory cartilages. Above the dorsal wall of the posterior cranial fossa may be seen two cartilages, lying close together, both small, but the left considerably smaller than the right. They may be known as the *cartilagines cranii posteriores*. Above each parietal plate, medial to the parietal bone, is seen an isolated nodule of cartilage, that on the right being larger and more elongated than that on the left; these may be called the *cartilagines cranii laterales*. Below and in front of the cranial pole of each cochlea there is a small, rounded mass of cartilage, which may be termed the *cartilago supracochlearis*.

CARTILAGE

Passing, next, to a consideration of the lateral aspect of the primitive skull (fig. 3), we note that it is made up of two main masses, dorsal (posterior) and ventral (anterior), almost separated by a large gap between the otic and orbitotemporal regions. The dorsal region is composed principally of cartilage, and presents a fairly smooth, convex, fenestrated surface, the most lateral part being formed by the rounded outer wall of the pars canalicularis of the otic capsule. Behind this the flat surface is seen to widen, and then quickly narrow, and to sweep backwards and inwards to unite with the corresponding plate of the opposite side in the tectum posterius. Above, the wall is heightened

by the reticular parietal bone (fig. 4). These structures enclose the lower and posterior portion of the cranial cavity.

The anterior mass is composed principally of the facial parts, and contrasts with the posterior in being narrower from side to side in its lower part, and in presenting a greater proportion of osseous material. Its surface is also much more irregular and uneven. In front of the pars canalicularis we see, in a recess which lies ventro-lateral to the two parts of the otic capsule, an irregular mass of cartilaginous and osseous structures, in which we recognize the anlagen of the auditory ossicles and the upper part of Meckel's cartilage, the latter appearing above the small tympanic and goniale (fig. 2), and being covered laterally by the squamo-temporalis. Below these structures, with its hook-like proximal extremity lying in a small cavity, but unconnected with the rest of the chondrocranium, is the slender shaft of Reichert's cartilage.

Above the otic capsule the large open space which will later form the middle cranial fossa is again apparent, and through this we see the lateral aspect of the hypophyseal fossa (fig. 3), with the high dorsum sellae, upon which are the ventrally projecting posterior clinoid processes, limiting it posteriorly. In the anterior wall of the sella turcica is the middle clinoid process (present on the right side only) and above this is to be seen the orbital wing of the sphenoid, the gentle curvature of the latter being broken by the anterior clinoid process, and its outer and posterior extremity terminated by a sharp process, projecting dorsally. Below the ala orbitalis, and separated from it by the wide and unclosed superior orbital fissure, is the ala temporalis, supported by a short processus alaris, the rounded extremity of the latter almost touching the ventral pole of the cochlea, and being quite close to the cartilago supracochlearis, which is plainly visible from the side.

Looking at the skull from a more anterior position we see, above, the cavity of the orbit, roofed over by the cartilage of the orbital wing of the sphenoid, and by the orbital portion of the frontal bone (fig. 4); limited medially by the shelving posterior portion of the ectethmoid; but widely open downwards and out-

wards, except where cut off by the zygomatic bone and the maxilla, and but imperfectly closed behind. In the posterior portion of the orbit is seen the elongated optic foramen, and the closeness of apposition of the sphenoidal and ectethmoidal cartilages is to be observed. An open space, communicating freely above with the orbit, below with the cavity of the mouth and medially with that of the pharynx, is seen in front of the ala temporalis, the medial wall of the space being indicated by the imperfectly developed vertical plate of the palatine bone and by the rudimentary medial pterygoid plate. The position of the as yet unformed pterygomaxillary fossa is indicated in this space by the sphenopalatine ganglion (fig. 14) (not shown in the model), and lateral to this, bounded by the incomplete zygomatic arch, are the temporal and zygomatic fossae. One is struck with the lack of prominence of the zygomatic region when compared with the osseous skull, the zygomatic bone and arch being completely overhung by the lateral part of the cranial floor. That this disproportion is partly due to the shallowness of the temporal and zygomatic fossae is evident from a comparison of the model with the bony skull. It would appear that the lateral growth of the ala temporalis of the sphenoid and of the zygomatic process of the maxilla, combined with thickening of the temporalis muscle, are the principal factors which bring about the widening of the temporal and zygomatic fossae, and consequent outpushing of the lateral parts of this area. It is evident from a comparison of the skulls of the newborn and the adult that this change continues till some time after birth.

The lower part of the facial region is characterized by the gaping cavity of the mouth, bounded above by the superior maxilla and below by Meckel's cartilage with its covering bone, the mandible (fig. 4). The lack of prominence of the angle of the latter, due to the shortness and inclination of the ramus and its relative nearness to the medial sagittal plane, may be observed, and it will also be seen that there is a small space between the articular process of the mandible and the position of the future glenoid cavity of the squamo-temporalis (fig. 4). The coronoid process of the mandible is quite close to the ala temporalis of the

sphenoid, medially, and to the zygomatic arch (as yet incomplete) laterally, a condition which does not obtain in the mature skull.

Dorsal to the prominent frontal process of the superior maxilla the isolated nodule of cartilage, known as the cartilago paranasalis, is to be seen, lying lateral to the cavity for the lacrimal duct and below the small streak of membrane bone, which is the anlage of the future lacrimal. Another smaller nodule of cartilage is seen near the back of the orbit lying against the upper surface of the ectethmoid and may be known as the *cartilago paraethmoidalis*. Separating the orbital from the nasal cavity is to be seen the shell-like ectethmoid, bearing upon its cranio-ventral aspect the small nasal bone. At the front of the nasal cartilages appear the open anterior nares, separated by the ventral border of the septum.

Regarded from below (fig. 2) the model shows in the foreground the mandibular (not shown in fig. 2) and upper part of the hyoid arches. Behind these we see the semi-cylindrical ventral surface of the planum basale, separated from the elongated, flattened, ovoid partes cochleares by deep furrows. It is to be observed that the anterior extremities of the latter do not project beyond the planum. The forked structure at the root of the planum, perforated for the hypoglossal nerve, is seen to be the anterior commencement of the flattened, ring-like sides of the foramen magnum, a downwardly projecting angle marking the position of the future occipital condyle. Lateral to and above the condyle there appears a stout cartilaginous process, which supports the lower and anterior part of the otic capsule. This is known as the processus paracondyloideus (Voit), and above it is seen a wide opening, the jugular foramen (fig. 4).

The two Meckelian cartilages (fig. 3) enclose an angle, rather sharp ventrally, in which are found the structures of the floor of the mouth. The inwardly curved palatine bones, with the assistance of the inner laminae of the pterygoid processes (fig. 2), imperfectly cut off the posterior part of the nasal cavity, and between the pterygoid laminae and the planum basale is seen the space occupied by the naso-pharynx (fig. 10). Attached to these medial laminae, and indeed developed from their caudal tips, are

the cartilagines parasphenoidales (Voit, '09), the representatives of the later hamular processes. The pterygoid laminae are quite separate from the alae temporales, which appear, from this viewpoint, as rhomboidal, perforated blocks.

Lying along the caudal border of the nasal septum are seen the anterior paraseptal cartilages in front, and the long thin plates of the vomer behind (fig. 2); and within each nasal cavity is a small mass of cartilage, lying in the middle meatus (fig. 12), to which the name *cartilago meatus medii* has been given and whose significance will be discussed with the regio ethmoidalis.

Summing up the cartilaginous and osseous structures which we find participating in the formation of the primitive skull, we have to consider a main cartilaginous mass, or chondrocranium, a number of accessory cartilages, the upper visceral arches, and the membrane bones.

The chondrocranium is a complicated mass of cartilage of exceedingly irregular formation, in which a number of definite areas may be recognized. Upon examination it is seen to consist of a larger dorsal and a smaller ventral enlargement, united by an isthmuslike part, the body of the sphenoid. A median stem, bent to enclose an angle of 115° open caudo-ventrally, forms the main axis, this being made up dorsally of the flattened planum basale and ventrally of the interorbital and nasal septa, or, employing the terms of Kölliker, the pars chordalis and the pars praechordalis respectively. These limbs are united by the corpus sphenoidale, or Balkenplatte of the German authors, which forms the apex of the angle. The four primary regions of the chondrocranium, which Gaupp has named, from behind forwards, the regio occipitalis, the regio otica, the regio orbitotemporalis and the regio ethmoidalis, are all represented in the median stem, in the order named, the first two being found in the pars chordalis and the second two in the pars praechordalis.

Springing out from the sides of the planum we have the walls of the posterior cranial fossa, while to the ventral end of the axis are affixed the side parts of the ethmoidal and orbitotemporal regions.

If the structures lateral to the ventral limb of this stem be removed, we have an object which roughly resembles a dipper or saucepan, the curved handle being made up of the ventral part of the stem, while the bowl, perforated below and at the sides, is formed ventrally by the planum basale, and laterally and dorsally by the walls of the posterior cranial fossa, the median lip being situated at the tectum posterius.

The chondrocranium is, at this stage, a continuous morphological unit, but there is histological evidence going to show that certain of its parts were primarily separate.

In addition to the chondrocranium proper a number of accessory cartilages, which have no direct connection with it and which have already been mentioned, also occur. They will be discussed in connection with the regions to which they refer, and are as follows:

Cartilago cranii posterior	Regio otica
Cartilago cranii lateralis	Regio otica
Cartilago supracochlearis	Regio otica
Cartilago parasphenoidalis	Regio orbitotemporalis
Cartilago paraethmoidalis	Regio ethmoidalis
Cartilago paranasalis	Regio ethmoidalis
Cartilago meatus medii	Regio ethmoidalis

Of the recorded human embryonic skulls that of Levi ('00) for the 28 mm. stage most closely resembles my specimen, but is somewhat younger. The next nearest stage, represented in the Ziegler model of Hertwig's 80 mm. embryo, is somewhat older.

The principal change which has occurred in the interval between the 28 and 40 mm. stages appears to be the development of the anterior cranial fossa. In the Levi specimen this is relatively narrower and deeper than in mine, thus indicating an adaptation of this region to the increasing size of the anterior part of the brain. Levi notes that this part of the skull has made more rapid development than any other in the interval between the 17 mm. and 28 mm. stages, and in the latter it is evidently still making rapid progress. When my model is compared with that of Hertwig, however, it is seen that in the period

between the 40 and 80 mm. stages the posterior fossa has made greater strides than the anterior, thus seeking to accommodate the enlarging, backwardly-growing cerebral hemispheres. The extent of development of the posterior portion of the brain-case in the interval between the 40 and 80 mm. stages will be realized when the ratio of the areas dorsal and ventral to the hypophyseal fossa, as they are found in the model of Hertwig and in my preparation, are compared. Although the dorsal area exceeds the ventral in my model the excess is by no means so great as it is in Hertwig's.

Speaking generally, since the 28 mm. stage of Levi there has been a flattening of the entire cranial floor. Between the 40 and 80 mm. stages the zone of greatest enlargement has been the upper edge of the posterior cranial fossa, the effect being as though this part had become stretched while the part around the foramen magnum had remained relatively stationary. The result is that the brain-case in this region has become more shallow and the sides more flaring, with their lateral and dorsal surfaces directed more caudally than outwardly. The region above the parietal plates has shared in this expansion, as is seen by the more widely placed parietal bones in the model of Hertwig, and this period of development has also witnessed the flattening out of the angle from the cranial aspect of the otic capsule, as may be seen when these skulls are compared.

Other expansive changes which have taken place in the interim between the 40 and 80 mm. stages are noted in the region of the middle ear, in the floor of the mouth, and in the temporal and zygomatic fossae, the details of which will be taken up in the discussion of the regions. In general one is struck with the large development of the cranial cavity, which gives to the Hertwig model a relative broadness when seen from the front, and has also resulted in a greater preponderance of the size of the cranium when compared with the facial region. A comparison of the Hertwig model with that of Jacoby for the 30 mm. stage brings out an even greater disproportion.

Of the skulls of other mammals those of Macacus cynomolgus and Semnopithecus maurus, modelled by Fischer ('03), may be

mentioned. The similarity in general outline is quite striking, when these are compared with my specimen. The illustration of the caudal aspect of the skull of Macacus shows a flattened condition of the partes cochleares closely analogous to that which obtains in my model. Though the dorsal part of the cranium is relatively shorter it is very suggestive of the cranium of homo, especially from the rudimentary condition of the side-walls.

CHONDROCRANIUM

Planum basale

That portion of the central stem of the chondrocranium which forms its dorso-caudal limb and is traversed medially and longitudinally by the notochord, is known as the planum basale (figs. 1, 2 and 5). It is an elongated and unperforated plate of cartilage of varying thickness, which extends from the intercondylar incisure of the foramen magnum to the dorsal border of the hypophyseal fossa, and forms the most dorsal part of the skull-base. Its cartilaginous substance is directly continuous with that of three regions; with the occipital region caudo-dorsally where the planum is seen to pass over into the lateral portions of the occipital anlage, with the orbitotemporal region cranio-ventrally, where it coalesces with the body of the sphenoidal cartilage at the dorsum sellae, and with the otic region laterally. The entire lateral border, with the exception of the extreme upper portion, is united to the pars cochlearis of the otic capsule, the line of union being indicated upon the medial surface of the latter by an elongated, narrow, crescentic strip (fig. 7). This line of union is formed of cartilage throughout, and in its cranial two-thirds this is of the same character as that of the adjoining parts. In the lower third, however, there is to be seen, microscopically, a distinct but thin sheet of younger cartilage, separating the adjacent parts of the planum and the cochlea, this being the last indication of the primitive separation of these parts.

It is worthy of note in passing that the 17 mm. stage of Levi shows the first indication of a union in the human skull between

the otic capsule and the planum basale, the cranialmost extremity of this bridge being the first to appear.

Encircling the zone of union of the pars cochlearis with the planum is a well-marked groove. The posterior portion of this, which may be known as the *dorsal basicochlear groove* (fig. 5), is crescentic in outline, and is fairly well defined. It contains the inferior petrosal sinus, and appears more sharply marked than in the models of Levi and Jacoby, judging from the illustrations of these authors. The ventral portion—much deeper and narrower—is also crescentic, and may be termed the *ventral basicochlear groove* (fig. 2). These grooves meet, above and below, their confluences being marked by notches, designated the *sphenocochlear* and *occipitocochlear notches* (fig. 5) respectively. The sphenocochlear notch occupies the interval between that part of the lateral surface of the corpus sphenoidale which lies dorsal to the processus alaris, medially, and the medial aspect of the cranial pole of the pars cochlearis, laterally (fig. 1). It is narrow and deep. The occipitocochlear notch is the ventromedial extremity of the jugular foramen.

Viewed from behind (figs. 1 and 5) the planum is seen to be concave from side to side in its lower two-thirds, and caudocranially throughout its entire extent. The cranial third of the dorsal surface terminates above in the crista transversa, a transverse ridge from which the dorsum sellae springs upwards, and which, according to Voit, may be taken to mark roughly the boundary between the body of the sphenoid and the otic or upper portion of the planum basale. This area of the dorsal surface is convex from side to side, and covers the part of the planum which has been called the clivus of Blumenbach. The lower portion of the planum is quite steep, but the cranial portion is much more so, the inclination thus agreeing with the description given by Levi for the 28 mm. stage.

The ventral surface of the planum (fig. 2) is convex from side to side, and almost straight caudo-cranially. It is thus evident that the caudal and cranial extremities are thicker than the middle portion, the latter being in the position of a primitive gap in the cartilage as shown by Levi in the 13 mm. and 14 mm.

stages and by Froriep in the 17.5 mm. stage, the latter having found the planum broken by a gap, filled with perichondrium, 1.9 mm. behind the canal of the hypophysis. This was just dorsal to the region where the occipitopharyngeal ligament, which had disappeared in older embryos (Levi), was inserted. This primitive gap (of which there is no evidence in my model, except the relative thinness of the cartilage in this region—and in this my findings agree with those of Levi and Jacoby for the 28 mm. and 30 mm. stages respectively—marks the site of the division which exists in early stages, between the two constituent parts of the planum, viz., that lying below it, belonging to the occipital region and representing the anlage of the future basi-occipitalis, and that lying above it, the clivus of Blumenbach, which is destined to form the basi-sphenoidalis, and has been included in the otic region.

The connection of the clivus with the body of the cartilaginous sphenoidal anlage is very primitive, according to the investigations of Levi upon young human embryos, as in the 13 mm. stage it is present while as yet there is no cartilaginous otic capsule in existence. This circumstance, combined with the relationship of the clivus to the basi-sphenoidalis of the osseous condition would seem to indicate that the upper portion of the planum should be grouped with the regio orbitotemporalis rather than with the regio otica, and this has been done by Levi, Jacoby and Van Noorden, but since Gaupp has more recently shown that the upper portion of the planum is more properly included with the otic region, and as several authors have since followed this course for the mammals (Voit, Mead) I shall adopt it in this description. The more minute details of the occipital and otic portions of the planum will be considered in the discussion of these regions.

The material composing the planum basale is mature cartilage, of uniform character, excepting one small, isolated mass of enlarged, vacuolated, cartilage cells, the nuclei of which appear larger and more darkly-staining than those of the surrounding areas, and the ground-substance of which has stained a dark

purple, thus standing in sharp contrast to the bluish matrix of the cartilage. This mass appears to be opposite the first part of the sub-basal course of the chorda dorsalis, and lies just ventro-caudal to the middle of the long axis of the planum. It belongs to the occipital portion, and is separated from the perichondrium by a thin sheet of mature cartilage. The perichondrium in the vicinity of this mass is unchanged, and contains no osseous tissue. In the 28 mm. stage of Levi the cells were, in this area, very large, and were surrounded by a very prominent capsule. We have in this area, no doubt, the beginning of the endochondral ossification center of the basi-occipitalis, which is said by Mall ('06) to appear on the 65th day.

The course of the chorda dorsalis has become familiar through numerous investigations, and I have nothing to add concerning it. The condition which I find agrees essentially with that illustrated by Fawcett for the 21 mm. stage (Fawcett '10a, fig. 2). The site of the future ligamentum suspensorium dentis, at the apex of the intercondyloid incisure, is marked by a coiled condition of the notochord, which corresponds to an intervertebral disk.

In my model the caudal portion of the planum is but slightly wider than the cranial, a condition which stands in sharp contrast to that found in the model of Hertwig, where one notices that, though the entire planum has undergone a widening, the region bordering the primitive foramen magnum has outstripped the more cranial portion in this regard. This broadening has, of course, separated the caudal extremities of the ventral and dorsal basicochlear grooves. The latter are both shallower and less strongly marked than in my model, as are also the sphenocochlear notches. Further, the side-to-side concavity in the model of Hertwig is almost obliterated, as is also that from above downward, and the inclination of the planum in the latter model is less steep than in mine.

Regio occipitalis

The occipital region has, in general, the form of a ring, whose irregular circumference, stoutly built and steeply sloping ventrally, plate-like and gently shelving dorsally, encloses the lower part of the posterior cranial fossa, the floor of which is perforated by an elongated fissure, the primitive foramen magnum (fig. 1). Its appearance suggests the occipital bone, of which it is the cartilaginous precursor.

Ventrally the ring is completed by a dorsally concave plate of cartilage, the basilar portion of the occipital anlage, which has been described as the lowermost part of the planum basale. As we have seen, the basilar portion is directly continuous cranially and laterally with the regio otica; below it splits to form the condyloid or lateral portions of the regio occipitalis, which spring downwards, outwards and slightly backwards and enclose, with their deviating, flattened limbs, the incisura intercondyloidea, marking the ventralmost part of the primitive foramen magnum. Reaching the most caudal points of the primitive skull at the paired, downwardly projecting ventral foraminal prominences (figs. 2 and 3), upon the site of the future condyles of the occipital bone, they suddenly bend upwards and outwards, twist on their long axes so that the inner surfaces, which before looked dorsomedially now look principally cranially, and at the same time they broaden ventrally and laterally, their outermost borders coming to underlie and support the partes canaliculares of the otic capsules. The lateral wing-like plate, which is thus formed on each side, is really the ventral and narrowest part of the squamous portion, and is known as the lamina alaris (Voit) (fig. 5). Ventrally it terminates in the prominent processus paracondyloideus, (figs. 2, 3 and 4) which may be seen from the front projecting laterally from the outer surface of the condyloid portion; dorsally it broadens into the squama, which becomes steeper, and swings medially to pass into the tectum posterius (fig. 5). The upper border, after skirting the dorsal surface of the ear capsule, passes backwards and inwards, being continuous above

with the lower border of the parietal plate; the lower border forms the lateral and dorsal boundary of the primitive foramen magnum.

When regarded from the front (fig. 2) the lateral or condyloid portions appear as paired, caudo-lateral extensions of the planum basale, their outer surfaces being simply continuations of the ventral convex surface of the planum; or, stating the same thing another way, if the anterior surface of the planum be regarded as a section of a cylinder, then the outer surfaces of the lateral portions may be looked upon as localized widenings of the same. The upper boundary of each may be arbitrarily marked off by a line drawn from the tip of the occipitocochlear notch to the ventral foraminal prominence (fig. 5), cutting just ventral to the hypoglossal canal, and representing approximately the line of separation which exists between these elements as they occur in their osseous condition at birth. The caudal portion of the planum thus includes the intercondylar incisure. Piercing the outer surface of the lateral portion, which looks ventro-laterally, is seen the outlet of the hypoglossal canal (fig. 2). Upon reaching the external edge of the latter the outer surface becomes narrow, and passes directly outward upon the aforementioned processus paracondyloideus.

Seen from behind, the inner surfaces appear as caudolateral continuations of the side-to-side concavity of the dorsal surface of the planum (figs. 1 and 5). They look medially, dorsally and somewhat cranially, and present the inlet of the hypoglossal canal. The lower borders are by far the thicker, and form the lateral limits of the incisura intercondyloidea, and each, as has been noted, passes over the ventral foraminal prominence to be thence continued dorsally as the lateral border of the foramen magnum (fig. 2). This portion of the border of the foramen, and the lower border of the condyloid portion, much resemble one another in thickness and roundness on cross-section, and when the skull is regarded from the side the ventral foraminal prominence, formed by their approximation, appears as the apex of an angle directed downwards and slightly forwards (fig. 3).

The rounded upper border broadens dorso-laterally and bifurcates to enclose the hollow jugular recess (fig. 5), the ventral limb passing laterally to become the ventral border of the processus paracondyloideus (figs 2. and 4), while the dorsal is marked, at its termination, by a small eminence, the anlage of the future jugular tubercle (fig. 5).

The hypoglossal canal, whose inlet and outlet have been noted, pierces the condyloid portion in a direction from within outwards and forwards. It lies rather nearer the upper than the lower border, between the jugular tubercle above and the ventral foraminal prominence below. The right canal is unpartitioned, but the left presents a bar of cartilage which separates its inner third into cranio-ventral and caudo-dorsal inlets. This bar has a general direction from above downwards, forwards and inwards (fig. 5). The outer two-thirds of this canal is not divided.

When the sections are followed from behind forward it is noted that two fasciculi of the hypoglossal nerve come into close apposition, one with the other (though they remain, for a time, separated by their sheaths), just dorsal to the entrance of the hypoglossal canal. These are of about equal size, and pierce the dura as a single strand, to enter the canal (on the left side the caudo-dorsal inlet) after a short sub-dural course. A third strand, equal in size to the first two combined, may be seen to pierce the dura shortly after the first two, but remains separated from the latter (on the left side by the aforementioned septum) while traversing the canal. Upon emerging the strands unite and shortly after their exit they become intimately associated with the vagus. In the canal they are accompanied by some small veins—the anlage of the rete of the hypoglossal canal—and a small artery. The great bulk of the canal space is, however, filled with loose connective tissue.

The processus paracondyloideus,[1] already referred to more than once, forms a conspicuous object as it springs from the

[1] It may be here noted that Voit uses the term "processus paracondyloideus" to apply only to the outer projecting tip (as it is found in the skull of the rabbit) of the structure which I have designated by this term. Mead, in describing the skull of the pig, uses the name "processus paroccipitalis" with the same meaning

outer surface of the condyloid portion just lateral to the hypoglossal canal (figs. 2 and 4). The straight line which joins the outermost tips of the processes passes through their roots also, and meets the median sagittal plane at a right angle, thus showing that each process is perpendicular to the sagittal plane of the head. The coronal plane in which this line lies cuts the ventral foraminal prominences. Each process is prismatic in shape, and thus presents three surfaces, which meet at the most lateral point, or tip. The medial part of the cranial surface is hollowed for the recessus jugularis; the lateral part lies outside of the cranium (fig. 4), its convex area forming the outermost termination of the caudal delimitation of the jugular foramen. Immediately above this convex surface appears the proximal, curved end of the cartilage of Reichert. The remaining surfaces look ventro-caudally and dorso-caudally respectively, and are separated by the caudal border, which projects downwards in a ridge-like manner (figs. 2 and 3), and forms a prominent object, when the skull is regarded from below, as it springs laterally from the outer part of the ventral foraminal prominence. The dorsal border is continuous with the lamina alaris. The ventral border is free (figs. 2, 4 and 5), and is thin in its medial half, where it bounds the recessus jugularis ventrally. From within outwards it follows a curved line, convex ventrally, and, in the region of the recessus jugularis, there is a small cranial concavity, over which the jugular vein and accompanying nerves pass. As has been observed before, this ventral border is the anterior extension of the bifurcated upper border of the condyloid portion.

The left process presents a slight difference when compared with the right. A small foramen (figs. 2 and 5) is seen to tunnel under its ventral border, thus forming a passageway from the recessus jugularis within to the ventro-caudal surface of the process on the outer aspect of the skull. The outlet lies just lateral to that of the hypoglossal canal. Though the right side

as Voit gives to the term "processus paracondyloideus." I have selected the latter term, and used it in a more extended sense, as applying to the entire structure corresponding to the transverse (and perhaps costal) process of the occipital vertebra, since this represents a morphological unit.

does not present this foramen the cartilage in this locality is very thin. The foramen contains nothing but loose connective tissue and its direction is from within downwards and forwards. It may be known as the *paracondyloid foramen*, and appears in the model of Hertwig on the right side only.

The squamous portions form the dorsal, and most of the lateral, part of the occipital ring. The architectural, and, as we shall later see, possibly the developmental foundation of each half, is the crescentic bar of cartilage which forms the lateral boundary of the primitive foramen magnum, and extends between its two prominences (figs. 1, 2 and 5). Rounded in cross-section it is seen to diminish in size gradually and uniformly from before backwards. Ventrally it is directly continuous with the condyloid portion (and may even be looked upon as a backward extension of this), the area of union being marked by the anlage of the future condyle, which has been termed the ventral foraminal prominence. Its principal direction is dorsal and slightly cranial, in contrast to that of the condylar portion, which, as has been noted, is caudal, lateral and slightly dorsal. Its concavity looks medially and slightly caudally, the latter curvature being evident when the skull is regarded from the side (fig. 3). Dorsally it terminates in the paired dorsal foraminal prominences, which mark the entrances into the incisura occipitalis superior. As will be seen later this bar corresponds to the neural arch of the occipital vertebra, and will be hereafter referred to as such. Medial to it is the anlage of the future medulla oblongata. Just above its ventral portion appears the jugular tubercle, and, upon examining the cartilage in this location, the cells are seen to present, from the dorsal part of this tubercle to a point about midway between the foraminal prominences, a condition similar to that which obtains in the central part of the basilar portion. This would seem to point to the beginning endochondral ossification of the ex-occipital portion of the occipital bone, the center for which, according to Mall ('06) appears on the 56th day. The ventral part of this center is confined to the jugular tubercle, but, as the sections are followed backward, it is found that it gradually comes to involve the entire core of the neural arch. The involve-

ment in ossification of the jugular tubercle is to be noted, as this, as we shall later see, is probably to be regarded as the superior articular process of the occipital vertebra.

Springing laterally and dorsally from this neural arch we find the upward-shelving squama, which narrows ventrally into the lamina alaris, and dorso-medially participates in the formation of the tectum posterius. Its lateral portion is widened. The upper border of the squama may be divided into ventral and dorsal portions, the former being connected with the otic capsule, and the latter with the parietal plate (figs. 3 and 5). The ventral part is fitted closely to the caudal and dorsal surfaces of the pars canalicularis of the otic capsule, the line of union being crescentic in shape, with concavity looking upward, forward and outward. This border extends cranio-dorsally from the outer angle of the jugular foramen to the fissura capsulooccipitalis (Voit), and its position is marked on both the inner and outer aspects of the skull by crescentic grooves, formed by the approximation of the flattened occipital and rising otic surfaces. These furrows, which may be known as the *medial* and *lateral capsulo-occipital grooves* (figs. 3 and 5), are not equally well marked, that on the inside of the skull being much the deeper. It contains part of the transverse sinus.

Evidence of an earlier separation between the pars canalicularis and the squama is afforded by the microscopic appearance. Between these structures there is seen, ventrally, a thin sheet of perichondrium, its plane being parallel with the transverse planes of the head, and when the sections are followed dorsally this is found to give place to a cartilage of younger type than that surrounding it, this being traceable almost as far back as the capsulooccipital fissure. The younger condition of the intervening tissue in the region of the jugular foramen as compared with that farther back would seem to indicate that fusion of the parts has taken place in the more dorsal part first, and has gradually progressed forward, and this assumption is born out by examining the illustrations of Levi. In his 14 mm. model (which is the earliest stage in which the otic capsule appears) the pars canalicularis and squama are almost entirely separated

by an elongated fissure extending from the jugular foramen to a small bridge of cartilage which cuts off the capsulo occipital fissure, and it is believed that this long cleft represents the metotic fissure of the lower forms. Upon examining the illustration of Levi's 17 mm. stage it is found that the aforementioned small bridge of cartilage has considerably widened ventro-medially, and in the subsequent 28 mm. stage the squama and the pars canalicularis are united as far as the jugular foramen. In both the 17 and the 28 mm. stages of Levi the union was marked by a separating sheet of perichondrium.

At the caudo-ventral extremity of this union there is seen a small notch, passing laterally from the outer part of the jugular foramen to lose itself upon the external surface of the skull, just above and behind the tip of the paracondyloid process.

It may be noted that the otic capsule, between its dorso-lateral connection with the squama and its ventro-medial connection with the planum basale, forms a bridge, uniting these structures, roofing the recessus supraalaris, and affording an upper delimitation for the foramen jugulare.

Dorsal to the capsulooccipital fissure the upper border of the squama proceeds backwards and inwards, and describes a curve with concavity upwards, to reach a small eminence, seen in the Hertwig and other models, which may be known as the *dorsal occipital prominence* (figs. 1 and 2). Beyond this it falls away to join with the upper border of its partner of the opposite side, this junction resulting in the formation of a dorsal concavity, directed upwards, which marks the upper edge of the tectum. Between the capsulooccipital fissure and the dorsal occipital prominence the squama is continuous cranially with the parietal plate. The line of union of the two lies at the bottom of a groove, seen from the inner aspect of the skull. It may be known as the *occipitoparietal groove* (fig. 1) and presents, on the right side two perforations, on the left one, through which small veins pass. The paired foramen (known as the *occipitoparietal fissure*, (figs. 3 and 5), is the larger, is elongated, and is situated about midway between the extremities of the groove. It perforates the groove at the most caudal part of its course. The smaller

foramen, which is limited to the right side, appears just in front of the larger. On the right side the terminal fourth of the upper border of the squama is separated from the slender dorsal tip of the parietal plate by a narrow slit. The parietal plate appears to end freely, but dorsal to this there are what appear to be degenerating cartilaginous cells, connecting the end of the parietal plate with the squama. This may indicate that these structures were united at an earlier time.

I regret that the dorsal extremity of the head of my embryo is missing, and that I am, on that account, unable to ascertain the condition in this region. On the right side the sections terminate in the dorsal occipital prominence, and show that the parietal plate has come to an end before this, as described. Owing to the fact, however, that the sections were cut obliquely, being deeper on the right side than on the left, I am unable to say whether or not the termination of the left parietal plate, and the relations which it bears to the squama, are the same as those found on the right side. I have, however, assumed that they are, and have so constructed my model; this having been done there was only the gap between the dorsal occipital prominences to be filled in, and this I did by reference to the Levi illustrations and Hertwig model. There are indications, on the left side, that the separation of the posterior extremity of the parietal plate will take place, as it has on the right, the cartilage connecting it to the squama, in the last few sections, being very thin.

In the membrane just lateral to the tip of the right parietal plate and dorsal occipital prominence there appears the weakly staining spicule of the interparietal bone. I have not represented it in the model, since only a small fragment is available, the remainder being included in the missing sections.

The sections go back sufficiently far to show that the occipital squamae unite dorsal to the tip of the superior occipital incisure, to form the tectum posterius, thus differing from the findings of Voit ('09) in lepus, who states that the squamae never reach the midline, the edges of the superior occipital incisure being the dorsal borders. I am, of course, unable to ascertain the exact width of the tectum.

The ventral part of the lower border has been described as the neural arch. Dorsal to this the character of the border changes completely, for, after the dorsal foraminal prominence is passed it loses its thickness and roundness on section, and becomes thin and serrated. This portion borders the superior occipital incisure, and really represents the lower portion of the original dorsal border, the upper portion being united to form the tectum posterius. The latter, according to Levi's investigations, is formed somewhere between the 14 and 17 mm. stages by dorsal fusion of the squamae.

The surface outlined by the above-described boundaries has been seen to become narrower ventrally in the lamina alaris (fig. 5). This is a wing-like plate of cartilage, bounded ventrally by the processus paracondyloideus. The outer edge of its upper surface bears the caudal extremity of the pars canalicularis of the otic capsule, and medial to this the upper surface, which looks principally cranially, participates ventrally in the structure of the hollow recessus jugularis, and forms the floor of the recessus supraalaris. The latter is a cleft between the lamina and the overhanging pars canalicularis of the otic capsule (fig. 5) through the lateral part of which the transverse sinus passes. The lower surface of the lamina alaris is also hollowed in the more central parts of the paraforaminal area (fig. 2, p. 372), and the plate is, therefore, quite thin—in fact on the right side it is perforated by a minute foramen, just lateral to the neural arch (fig. 1), and posterior to the jugular tubercle, through which a small vein passes. This foramen is doubtless the representative of the condylar foramen of the adult condition. Dorsally the lamina alaris becomes wider, thicker, and more vertical in slope, as it passes into the larger posterior portion of the squama. The inner surface is smooth, and presents, dorso-lateral to the tip of the superior occipital incisure a small oval foramen on the right side, but not on the left, through which a small vein passes (fig. 1). A very shallow groove runs parallel to the neural arch, just lateral to its upper aspect.

Upon the outer surface the most prominent object is a rounded eminence,—*the lateral occipital eminence*—(fig. 3) which appears

immediately dorsal to the otic capsule, and is separated therefrom by the cranial portion of the lateral capsulooccipital groove. Its posterior part projects slightly into the cranial cavity (fig. 5), and its edges are ill-defined, fading gradually into the surrounding cartilage. This marks the thickest part of the squama. It may be followed caudally as a low ridge on the outer surface, and is seen to meet, almost at a right angle, a second ridge, which extends from the tip of the paracondyloid process to the dorsal foraminal prominence, and to which the name *crescentic ridge* (figs. 2–3) may be given, the point of union being about the center of the latter.

The crescentic ridge, seen only on the outer surface of the skull, is a low elevation which sweeps dorsally and medially, between the extremities above mentioned, and in so doing describes a curve with convexity backwards and outwards. At its ventral end it is sharply defined, and is separated from the ear capsule by the small notch which stretches outward from the jugular foramen. Dorsally it is wider, and its margins are not so clearly outlined. It is of considerable thickness throughout, and is the lateral boundary of a semi-crescentic area—well seen in E. Fischer's ('03) illustration of the skull of macacus cynomolgus, and also in Voit's picture of the skull of lepus—which may be known as the *paraforaminal area* (fig. 2). It is bounded medially by the rounded edge of the neural arch, and ventrally by the caudal border of the paracondyloid process. Its hollowed central portion, which represents the lower surface of the lamina alaris, has been before referred to, and on the right side has been seen to be perforated by the minute condylar foramen. We find, therefore, that the thickest parts of the squama are situated immediately behind and below the ear capsule, and are represented by the lateral occipital eminence and the crescentic ridge, the former, just behind the capsulooccipital fissura, being slightly the thicker. The area dorsal to a line passing from the dorsal foraminal prominence to the occipitoparietal fissure is very thin, and presents a short distance behind this line evidence of commencing ossification. The cartilage appears to be undergoing greatest change in the region immediately dorso-lateral to the tip of the superior

occipital incisure, and dorsally the modified cartilage may be traced as far as my sections go. This area no doubt represents the center of ossification of the supraoccipital, which according to Mall ('06) ossifies from four centers, the first pair appearing in the region immediately dorsal to the foramen magnum on the 55th to 56th day, and being followed by other paired centers in the region ventral to this.

In all there have been noted in the occipital region five commencing centers of ossification, one, median, for the basilar portion; two, lateral for the condyloid portions, and two, lateral, for the squamous portions. In the vicinity of these centers the cartilage grades off into that surrounding them. Of the rest of the cartilage it may be noted that the material of the ventral border of the paracondyloid process, of the ventral part of the jugular tubercle, and of the body of the condyloid portion lateral to the hypoglossal canal shows a more advanced character than the remainder.

The atlantooccipital capsules are present; each is a sac composed of a dense sheet of perichondrium, covering the applied facets of the atlas and condyloid portion of the occipital cartilage. They are richly cellular, and above them the cartilage is of a younger type than that found in the remainder of the mass, but gradually grades off into the more mature type.

The primitive foramen magnum (figs. 1–2) is, at this stage, worthy of examination. It consists of three parts; a large central area, with which are continuous ventral and dorsal incisures. The central portion is bordered by the crescentic, rounded neural arch, and its plane looks upward and slightly forward. Ventrally is to be seen the intercondyloid incisure, its plane looking dorso-cranially, and this plane forms an angle with the main portion, which is open cranio-dorsally. This incisure remains a part of the foramen, later undergoing widening, and rounding out at the tip, as may be seen by examining the Hertwig model and the osseous skull. Behind the central portion, and appearing as a dorsal prolongation of it, is the superior occipital incisure, filled by the membrana atlanto-occipitalis dorsalis. The plane of this incisure is somewhat

steeper than that of the part in front, and thus it forms an angle, looking cranially and slightly ventrally, with that of the main area. This is shown upon the lateral contour of the skull as the point of an angle, directed downward and backward, marking the tip of the dorsal foraminal prominence (fig. 3).

The superior occipital incisure, though representing the dorsal part of the primitive foramen magnum, is by no means a part of the adult foramen magnum, as its edges unite later to complete the caudo-dorsal closure of the occipital region, the dorsal limit of the foramen magnum becoming set by the approximation of the dorsal foraminal prominences, as shown by the researches of Bolk ('04).

I find no evidences of the condition which Bolk describes at the posterior extremity of the foramen magnum, viz., a central cartilaginous mass (formed by the fusion of paired pre-existing masses) which lies between the upturned dorsal extremities of the occipital side-walls.

It seems clear from the work of various investigators, beginning with Froriep ('86), that although the occipital region of the mammals has been developed from the skeletogenous elements of four metameres, only the most caudal ever attains the status of a mature sclerotome, the three cranialmost being undifferentiated and playing but a minor part in the construction of the adult bone. This being true it follows that the story of the evolution of the occipital anlage is largely the story of the development of the caudal segment, or, as it will be hereafter called, the occipital scleromere or primitive occipital vertebra.

As in the spinal region, so in the occipital, the sclerogenous tissue passes through successive and overlapping membranous or blastemal, chondrogenous and osteogenous phases (Bardeen '05, '08), and in each phase the condition in the occiput recalls that of the corresponding phase in the vertebrae. Thus in the blastemal stage the occipital scleromere shows paired chordal processes joining across the midline in the region of the notochord, and paired neural processes embracing the neural canal as in the spinal scleromere; the costal processes are, apparently, poorly developed in the occipital scleromere. But along with this

marked similarity to the vertebrae the occipital scleromere shows certain individual peculiarities. Instead of uniting with the cranial portion of the segment immediately caudal to it, after the fashion of the other scleromeres, it retains its connection with the cranial portion of its own segment, and this, in turn, becomes united with the tissue of the three cranial, undifferentiated sclerotomes, the membranous anlage thus formed being known as the occipital plate (Bardeen '08 and '10). According to Froriep the occipital scleromere is marked off from the undifferentiated sclerotomes by the caudal root of the hypoglossal nerve.

The middlepiece of the occipital plate is made up in its caudal portion of the chordal processes of the occipital scleromere, and in its cranial part it also contains the elements of the body masses of the undifferentiated segments. So also while the lateral portions are mainly formed of the neural processes of the occipital scleromere they also contain, in the region cranial to the hypoglossal canal, remnants of the condensed lateral masses of the undifferentiated segments (Froriep, Levi).

In the chondrogenous stage of the occipital anlage of man, for the knowledge of which we are principally indebted to Levi, there are also striking resemblances to the vertebral conditions. The 13 mm. stage, studied by this author, shows the beginning of the transition from the membranous to the cartilaginous condition and in this paired masses of condensed chondrogenic mesenchyme, separated by the perichordal septum, were situated dorso-caudally in the middlepiece or basilar portion, and in the dorsal part of each mass, medial to the hypoglossal nerve, a small cartilaginous nodule occurred, recalling the paired chondrous centers of the body of a spinal vertebra. The mesenchymatous masses, representing the chordal processes of the occipital scleromere, were joined ventrally; they are the first portions of the occipital anlage, and indeed of the entire chondrocranium, to undergo chondrification, and eventually form the diverging, caudolateral portions of the pars basilaris bordering the foramen magnum. In the matter of priority in time of chondrification

of the body over the arch processes the occipital scleromere resembles those of the atlas and axis.

In the 14 mm. stage of Levi chondrous paired centers for the neural processes of the occipital vertebra arise, lateral to the hypoglossal nerve roots, and speedily unite by continuity of cartilage with the nodules just mentioned, which also join with one another in the same way, at first ventrally. The fused basilar centers are a little later joined by the chondrifying middle part of the undifferentiated sclerotomes to form the median part of the pars basilaris, and the chondrifying lateral masses of the undifferentiated sclerotomes join the neural processes. Thus the basilar portion, which may be taken to extend to the ventral margin of the hypoglossal canal is built up from the middle parts of all of the primitive occipital segments, the portion included in the anterior margin of the foramen magnum arising from the body mass of the occipital scleromere, and the cranioventral part coming from the body masses of the undifferentiated sclerotomes.

A lateral outgrowth from the neural arch is seen in a membranous condition in the 13 mm. stage of Levi, and is somewhat later in chondrifying than the neural arch of either the occipital vertebra or of the atlas. It represents, doubtless, the transverse process of the occipital vertebra, and is spoken of by Levi as the Querleiste. The costal process of the occipital vertebra has not been shown to have a separate center of chondrification.

It is to be noted that in the 13 mm. stage of Levi the bodies of the occipital vertebra, atlas and axis are represented by paired masses of chondrogenic mesenchyme, separated by the perichordal septum, and each mass contains a small nodule of cartilage (except in the case of the axis, where the two nodules have fused), their neural arch processes being entirely membranous. In the 14 mm. stage of Levi not only are the bodies chondrified but also the neural arches; for in the occipital vertebra a chondrous center appears just lateral to the hypoglossal foramen, and the arches of the atlas and axis also present each a small nodule of cartilage. Thus chondrification takes place simultaneously in cor-

responding parts of the occipital and first and second spinal vertebrae.

The paired cartilages of the body of the occipital scleromere of Levi's 14 mm. stage appear to be slow in joining dorsally, being found separated in this region by the perichordal septum, while their ventral parts are united. This is possibly to be explained as a result of expansion in this region, from intracranial pressure.

The above identification of the cartilaginous neural arch of the occipital vertebra and its appendage, the transverse process, as found in the early Levi models does not agree with this author's own interpretations of his findings. In his earliest human skull, from a 13 mm. embryo, Levi shows, lateral to the roots of the hypoglossal nerve, what he calls the lateral portions, from whose lateral surfaces the Querleisten project directly outward, and he figures the latter in all four of his stages. In the 14 mm. stage he finds in each lateral portion, just external to the hypoglossal nerve roots (Levi, text fig. 2) a cartilaginous center, which speedily joins with that for the body mass, which latter, as has already been noted, represents the chondrification of the body of the occipital scleromere. It seems evident that the center of chondrification in Levi's lateral portion is the center for the neural process of the occipital scleromere, with possibly the addition of the center for the undifferentiated portion, and hence it follows that the club-like membranous mass in which this nodule is found is the neural process of the occipital scleromere, which, with its partner, builds the lateral part of the neural canal of the occiput. Furthermore, these lateral portions are in direct alignment with the spreading arch-processes of the underlying cervical vertebrae, as is shown by the illustrations of Levi, and, though this author does not label them as the arches of the occipital vertebra, Bardeen, in his copy of Levi's illustration of his 13 mm. stage in Keibel and Mall's "Human Embryology" (vol. 1, p. 401) gives them what I regard as the correct designation, "Arcus vert. occip." Though the lateral portions of the occipital vertebra are here considerably larger than the arches of a cervical vertebra this extra size is probably

a local adaptation. Again, at the same time (14 mm. stage) according to Levi the arch mass of the undifferentiated sclerotomes has chondrified. It would, indeed, be surprising if the neural arch of the occipital vertebra were still membranous at a time when the arch processes of the undifferentiated sclerotomes were chondrified (those of the atlas and axis being also chondrified), as would be the case if Levi's interpretation were correct. My identification obviates this difficulty.

Accepting this interpretation it follows that the small processes or Querleisten which project laterally from the lateral processes cannot be the tips of the neural arches, as Levi describes them; they are really the anlagen of the transverse processes of the occipital vertebra. Levi, who does not account for the dorsal tips of the lateral portions of the occipital vertebra at all, is led to conclude that the Querleisten represent the tips of the neural arches, apparently, by the histological resemblance of their tissue, in the early stages, to that composing the tips of the neural arches of the underlying cervical vertebra. He remarks, however, that the Querleiste is very tardy in chondrifying when compared with the neural tip of the atlas, a detail which is, if anything, opposed to his identification of it as the tip of the neural arch of the occipital vertebra, but is what might be expected if it be homologized with a transverse process. The Querleisten are shown in the Levi models to be in direct alignment with the transverse processes of the cervical vertebrae, and they never come together dorsally and unite, after the fashion of the dorsal extremities of the neural arches. They are identical with what I have called in my model the paracondyloid process, following Voit, who described similar structures in the rabbit, and identified them as the representatives of the transverse processes, also remarking that the rectus capitis lateralis muscle, which each has attached to its lower surface, is to be regarded as the morphological equivalent of an intertransversarius muscle. Mead ('09), too, finds a similar and very strongly marked process in the skull of the pig, and calls it the paroccipital process. Both Levi and Voit state, correctly I believe, that the process ultimately becomes the jugular process of the occipital bone.

My identification of the primitive elements forming the pars basilaris also is not exactly in agreement with Levi's, but the difference depends largely on where the line between the basilar and lateral portions of the occipital anlage is drawn. I have assumed the separation between these portions to be approximately as it exists at birth, while Levi includes in his lateral portions the nodules which I believe represent the paired body of the occipital vertebra. If my interpretation of these structures is correct they should be regarded as constituents of the basilar portion, which would thus represent the body masses of the undifferentiated sclerotomes plus the body mass of the occipital vertebra, while according to Levi's view it would represent only the body masses of the undifferentiated vertebrae.

In the later development of the chondrogenous stage the forerunners of the individual features of the occipital bone begin to show themselves, and we find cartilaginous representatives of the body, pedicles, inferior and superior articular processes, transverse (and possibly costal) processes, laminae and spinous processes, these almost altogether differentiating from the occipital scleromere. The development of the body (pars basilaris) has already been discussed. The pedicles are, of course, represented by the cartilaginous tissue in the region of the hypoglossal foramen, but here we have material added from the lateral mass of the cranial sclerotomes, (Froriep, Levi), which results sometimes in the partitioning of the foramen, as may be seen on the left side of my model, and as has frequently been found by other observers in young embryos of homo and other mammals. The inferior articular process is, doubtless, represented by what has been designated the ventral foraminal prominence, the forerunner of the condyle, though the condyle of the mature bone is partly formed by the pars basilaris. The rudiment of the superior articular process is, perhaps, to be seen in the jugular tubercle. The transverse process, as we have seen, is to be found in the paracondyloid process, and there is some evidence to indicate that in this latter there may be included the costal process as well. It will be remembered that the paracondyloid process was perforated on the left side by

the paracondyloid foramen, and that on the right side the corresponding area of cartilage was thin, and, further, that the Hertwig model also presented this foramen on one side. It pierces the process from above downwards and forwards and is in series with the costo-transverse foramina of the cervical vertebrae below. If it be regarded as the costo-transverse foramen of the occipital vertebra, then the bar of cartilage which closes it in front must be looked upon as the costal process of this vertebra. I have not been able to find that the costal process of the occipital anlage has a separate center of chondrification as it has in the spinal vertebrae. Though there is no vessel or nerve passing through the paracondyloid foramen yet it is possible that this represents an old channel of the vertebral artery, which has become obsolete on account of the change of course of this vessel. In this regard the foramen may be analogous to the costo-transverse foramen of the 7th cervical vertebra, which no longer transmits the vertebral artery.

I regard as the representatives of the laminae the crescentic, tapering, hornlike masses of cartilage which form the lateral borders of the foramen magnum, and which I have spoken of as the neural arches. Since the squamous portions are continuous with the outer borders of these they may be considered as extensions of the laminae, and the tips of the latter (dorsal foraminal prominences) as the representatives of the spinous processes.

Not only on developmental, but also on histological grounds, does it appear evident that the margin of the foramen magnum is formed from the primitive neural arch of the occipital vertebra. Upon an examination of my slides it is seen that the cartilaginous tissue of this portion bears a strong resemblance to that composing the arches of the upper cervical vertebrae, and even more striking is the situation of the ossification center. It appears, as I have described, in the arch of the occipital vertebra, just dorsal to the root of the transverse process—exactly the same relative position as the ossification center in a cervical vertebral arch occupies. This point is beautifully brought out in the model of Hertwig, where, upon either side of the neural canal a

series of ossification centers presents itself, the uppermost member of the series being found in the exoccipital, in the position in which I have described it in my model, and being followed caudally by the ossification centers for the 1st, 2nd, 3rd and 4th cervical vertebrae; each center being uniformly situated with reference to its respective arch. In the basi-occipital, too, the single median ossification center recalls the center of a typical vertebral body, and indeed the osseous elements of the occipital bone at birth are strikingly similar to those of a vertebra, especially the fifth lumbar vertebra.

Keeping in mind the intimate and peculiar relationship which a typical vertebral arch bears to the cord which it encloses it seems reasonable to suppose that this relationship would be retained even after the vertebra had been taken up into the skull. It seems much more reasonable, even on purely theoretical grounds, to assume that the arch of the occipital vertebra goes to form the margin of the foramen magnum of the mature skull than to postulate that it forms the jugular process, as Levi maintains, and when it is realized that the latter is formed from the transverse process of the occipital vertebra, and that the margin of the foramen magnum is merely the modified arch of the occipital vertebra the proper relationship of the parts becomes intelligible.

Not only do the neural arches of the occipital vertebra exhibit a striking resemblance to those of the cervical vertebrae in each stage which has been studied, but their behavior in growth recalls very strongly that of the arches below. This parallelism in manner and time of development between the arch of the occipital vertebra and those of the cervical vertebrae is clearly shown by an examination of the 13 mm., 14 mm., 17 mm., and 28 mm. stages of Levi, my own 40 mm. stage, and the 80 mm. stage of Hertwig. The neural arches of the occipital vertebra, small at first, are seen to grow backwards and outwards, and then to come together medially and dorsally, thus hedging in the dorsal part of the foramen magnum, this process being duplicated coincidently by each of the upper cervical vertebral arches.

In each successive stage the tips of the neural arches, both occipital and cervical (which retain their original alignment), are seen to be farther advanced than in the last in their enclosure of the spinal cord, a condition strikingly brought out by a comparison of the foramen magnum and the underlying vertebral arches of my model with those of the oldest Levi model, on the one hand, and the Hertwig model on the other. In the 28 mm. Levi model the tips of the neural arches of the occipital and upper cervical vertebrae are separated by a considerable interval, in my model they are almost united, and in the Hertwig model, as has been noted, they are all completely joined; in the adult bone the tips of the occipital vertebra are represented by the internal and external occipital crests (representative of a spinous process). This closure of the foramen magnum takes place, accordingly, somewhere between the 40 and 80 mm. stages in man, and it bears a striking resemblance to that of the segments of the spinal canal. Growth seems to progress uniformly throughout the series, and dorsal closure is apparently completed at about the same time in each segment. Thus, with the fusion of the dorsal foraminal prominences there is completed what amounts to the closure of the cranial extremity of the spinal canal.

From what has been said regarding the formation of the foramen magnum it will be evident that what is found in the 40 mm. stage is something more than the foramen of the adult condition; it is this plus the superior occipital incisure. Further, the structure described as the tectum posterius is not the dorsal delimitation of the real foramen magnum at all, but merely that of the superior occipital incisure. The edges of the latter unite in the form of a median seam upon the union of the dorsal extremities of the neural arches of the occipital vertebra, and thus is effected the closure of the portion of the floor of the occipital region dorsal to the foramen magnum. This conception of the development of the foramen magnum explains why the primitive foramen is relatively so much larger than the adult condition.

In the condition of the occipital anlage at birth we find a basilar portion, formed in its cranial part from the body mass

of the undifferentiated sclerotomes and in its foraminal portion from the body mass of the occipital vertebra. The exoccipitals have been developed, as we have seen, principally from the neural arches of the occipital scleromere, but in the region of the foramen hypoglossi there has been added material from the lateral masses of the undifferentiated scleromere. The supraoccipitals, which ossify separately, are to be regarded as primarily connected with the neural arch of the occipital vertebra, and their separateness of ossification is analogous to the condition which we find in the 5th lumbar vertebra.

Regio otica

The otic region, like the occipital, is transversely somewhat ringlike in form, and its irregular sides, for the most part flattened from within outwards, are united by their caudal edges with the upper border of the occipital anlage, except where sundry foramina occasion interruptions. The otic ring, accordingly, heightens the dorsal part of the cartilaginous brain-case. In it we recognize four distinct elements, two unpaired, the otic portion of the lamina basalis and the tectum synoticum, and two paired, the otic capsule and the lamina parietalis. In addition to the parts entering into the composition of the ring there are also to be considered in the otic region the small, paired, isolated nodules known as the cartilagines supracochleares, cranii laterales and cranii posteriores.

When the skull is viewed from within (figs. 1 and 5) the upper or otic portion of the lamina basalis is seen to unite the ventromedian portions of the otic capsules. Passing laterally the eye meets the large, irregular mass of cartilage known as the otic capsule, which forms the ventro-lateral delimitation of the posterior cranial fossa, as well as part of the floor of the middle cranial fossa. Caudo-laterally the capsule is continuous with the lamina alaris, and dorsal to this with the wider portion of the squama of the occipital anlage, while cranio-dorsally the commissura capsuloparietalis (figs. 3 and 5) is seen uniting the larger dorsal portion of the otic capsule with the lamina parie-

talis the latter having also a union with the capsule below the capsuloparietal fissure. Dorsal to the capsuloparietal commissure the flattened parietal plate appears, and we note that it is wide ventrally, but becomes narrow dorso-medially. With the parietal bone it assists in the formation of the wall of the cranium in this region. Below, the parietal plate is continuous with the upper border of the squama; dorsally it is represented in the model as terminating freely just before reaching the dorsal occipital prominence, but there is microscopical evidence, as far as my sections go (as I have already stated) which seems to indicate that there was here a previous union of parietal plate and squama. Of the unpaired, dorso-median tectum synoticum, described by several authors, I can, unfortunately, make no statement, as my sections for this dorsalmost region are lacking. The otic ring, as I have represented it in the model, is therefore incomplete dorsally. This may possibly be its actual condition, and in this connection it may be noted that Mead states that the otic ring in Sus is incomplete dorsally.

The pars otica of the lamina basalis, which is the most cranial part of the chordal portion of the base of the skull, has already been described. The fissura basicochlearis is incomplete above, being represented by the lowermost part of what I have designated the spheno-cochlear notch—filled with connective tissue and a few small veins. The abducens nerve passes above the notch, lateral to and below the outwardly-projecting posterior clinoid processes, and in this the condition is similar to that described in such mammals as the rabbit (Voit) and pig (Mead), except that the basi-cochlear fissure in the latter types is closed above by a cartilaginous bridge joining the upper surface of the pars cochlearis with the lamina basalis, the abducens nerve passing over this bridge. In the model of Sus by Mead this nerve passes throught a foramen formed by cartilaginous connection of the posterior clinoid process with the cochlea. There is no evidence of this in my preparation.

The connections of the otic capsule with the planum basale, squama occipitalis and parietal plate have been noted. The model also shows it continuous ventro-laterally with the incus,

but histologically a sheet of perichondrium intervenes. There is no connection with the processus alaris of the temporal region through the commissura alicochlearis, such as Jacoby shows in the 30 mm. stage of homo and Voit figures in his model of the skull of lepus, but there is what I regard as a rudiment of this, viz., the cartilago supracochlearis, (figs. 1 and 3) which will be later described. The otic capsule roofs over the recessus supra-alaris and recessus jugularis, and bridges the foramen jugulare (fig. 5).

In the otic capsule (figs. 6 and 7) we may distinguish a larger dorsolateral portion, which contains the semicircular canals, and which may therefore be known as the pars canalicularis (Voit), and a smaller, ventro-median portion, which contains the cochlear part of the membranous labyrinth, and which may therefore be termed the pars cochlearis. Voit has restricted the use of the term 'pars vestibularis' to the dorsal part of the pars cochlearis, which presents the fenestrae vestibuli and perilymphatica and the fenestrae for the vestibular division of the eighth cranial nerve. It contains the first, or unwound, portion of the ductus cochlearis. I shall adopt this usage of the term in this description.

The cartilage of the two portions is directly continuous, the zone of union being marked cranially by a notch, open above, which may be known as the *superior otic notch* (figs. 6 and 7), and ventro-laterally by a recess formed by the union of the lateral surface of the pars cochlearis with the ventral surface of the pars canalicularis; this may be known as the *ventro-lateral otic recess* (fig. 6). It contains the anlagen of the auditory ossicles.

The pars canalicularis is an irregular, somewhat flattened, ovoid mass of cartilage, hollowed for the passageways of the semicircular canals and utriculus. It presents for examination three surfaces, ventral, lateral and medial. Of these the lateral and medial are convex, and are approximated above and behind, their ventral edges being widely separated. The lateral surface (fig. 6) is smooth, and somewhat triangular in shape, being wider above than below. The cranial border is rounded, and is formed

by the out-bulging of the anterior semicircular canal; it is known as the prominentia semicircularis anterior. Ventrally this prominence terminates in the prominentia utriculo-ampullaris superior, a conspicuous rounded eminence at the cranio-ventral extremity of the pars canalicularis, marking the upper approximation point of its three surfaces. It is formed principally by the wall of the ampulla of the anterior semicircular canal (fig. 8). Springing upward from the dorsal part of the anterior semicircular prominence the capsuloparietal commissure may be seen, its connection with the otic capsule being shown in figures 6 and 7. Dorsal to this the border is marked by the capsuloparietal fissure (fig. 3), and caudal to this again by the lower union of the parietal plate with the otic capsule; under the latter union is to be noted the capsulooccipital fissure (fig. 7). The lowermost part of this border is formed by union with the squama. These borders separate the lateral from the medial surface of the capsule.

Both the capsuloparietal and capsulooccipital fissures appear in other models of the human skull (Levi, Hertwig), and they have also been shown to be present in the primitive skulls of other mammals, as the ape (Fischer) and rabbit (Voit). The capsuloparietal fissure is sometimes known as the foramen jugulare spurium, and the capsulooccipital fissure as the foramen petrosooccipitale.

The ventral border, which separates the lateral from the ventral surface, is, below the superior utriculoampullary prominence, marked off mainly by the conspicuous crista parotica, below this by the mastoid process, and below this again by the prominentia semicircularis posterior (fig. 6), which passes over the root of the mastoid process at this point.

The most prominent object upon the lateral surface is the *lateral otic eminence* (fig. 6), which lies in its dorso-cranial area, separated from the dorsal part of the anterior semicircular prominence by a very shallow groove. It slopes backward into the parietal plate between the two post-otic fissures, and is formed by the backward and outward projection of the massa angularis, a large mass of cartilage lying in the enclosure formed by the anterior and lateral semicircular canals, the crus com-

mune, and the upper part of the posterior canal (fig. 8). The two lateral otic eminences mark the extremities of the greatest transverse diameter of the primitive skull.

The dorsal extremity of the posterior semicircular prominence forms a gentle rise in the caudal area of the lateral surface, and then passes over the root of the mastoid process, as we have seen, to become prominent in its ventralmost portion, the prominentia utriculoampullaris inferior (figs. 6 and 7), which forms the conspicuous border between the ventral and medial surfaces and acts as the upper border of the lateral part of the jugular foramen.

The prominentia semicircularis lateralis is an indistinct swelling passing downward and backward from the crista parotica in the region of the incus to the dorsal extremity of the posterior semicircular prominence.

The medial surface (fig. 7) is more extensive than the lateral. Its cranial and dorsal borders are the same as those of the lateral surface; its ventral border is marked above by a rounded ridge passing downwards from the superior utriculoampullary prominence to the superior otic notch, and below by the posterior semicircular prominence, which, as has been seen, terminates ventro-medially in the inferior utriculoampullary prominence, the latter bearing a ventrally-projecting process, the processus interperilymphatica (Voit). The middle portion of the ventral boundary is formed by the transition of the medial surface of the pars canalicularis into that of the vestibular portion of the pars cochlearis. As has been mentioned the medial surface is convex, and presents in its central area as its most prominent object the prominentia cruris communis (Voit), formed by the crus commune within (fig. 9). Upon the dorsal part of this prominence is seen the long, almost horizontal, slit-like foramen endolymphaticum, for the outlet of the ductus endolymphaticus. Both lips of this foramen are formed of a young type of cartilage and it may be noted that the upper lip projects medially in its dorsal part to overhang the duct, and is continued dorsally past the foramen to form a groove, in which the duct lies (fig. 7). The dorsal extremity of this upper lip appears as a short, free process, overlying the duct.

The condition of the terminal portion of the ductus endolymphaticus is of interest. This does not end in a sac, but becomes a long, narrow fusiform dilation shortly after emerging from the foramen, and gradually decreases in size, to be prolonged, at its dorsal extremity, into a fine, lumenless filament or cord of cells. After leaving the foramen endolymphaticum it passes medial to the transverse sinus in the sub-dural space, outward and backward, and ends in the loose sub-dural connective tissue just medial to the occipitoparietal groove, about 1.8 cm. dorsal to the capsuloparietal fissure. It is not intimately associated with the cartilage of the ear capsule after its exit therefrom, and hence cannot retard the development of this locally to bring about a thinness of the wall, which is found in my preparation just dorsal to the endolymphatic foramen, in the area corresponding to that in which the small foramen which Voit describes in the developing otic capsule of the rabbit appears. This thin region of the wall (which is unperforated) is caused by encroachment upon it from within of the cavities surrounding the dorsal extremities of the anterior and posterior semicircular canals, and not by pressure of the saccus endolymphaticus from without, as Voit assumes in the skull of lepus.

The upper part of the medial surface is marked by the crescentic inner aspect of the anterior semicircular prominence (fig. 7), which is more distinct here than on the lateral surface, and sweeps backwards, from the superior utriculoampullary prominence to the dorsal end of the prominence of the crus commune. It corresponds to the arcuate eminence of the adult bone. Below this prominence is to be seen a distinct fossa, the fossa subarcuata anterior (Voit), delimited caudally by the prominence of the crus commune. This fossa invades the substance of the massa angularis, and upon examining the slides microscopically it is found that it is filled with a mass of loose connective tissue, covered by the dura.

The medial surface below the prominence of the crus commune looks downward, backward and inward in its upper portion, and almost directly downward in the lower. The latter is thin, composed of more darkly staining cartilage with thickset cells and little ground substance, and forms the roof of the supraalar

recess. In its ventral area may be seen the inferior utriculo-ampullary prominence, continuous dorso-laterally with the posterior semicircular prominence and ventrally with the short interperilymphatic process. A spur of the inferior utriculo-ampullary prominence caused by a localized thickening of the wall, projects backwards and upwards as a low ridge to disappear somewhat below the endolymphatic foramen. It overhangs the transverse sinus in this region. The fossa subarcuata posterior, which Voit mentions in his description of the skull of the rabbit, is not represented here.

The boundaries of the ventral surface (fig. 6) have already been described in connection with the discussion of the ventral boundaries of the lateral and medial surfaces. Its medial part is concerned with the junction of the pars canalicularis with the vestibular portion of the pars cochlearis. The lateral part of the ventral surface forms the dorsal wall of the ventro-lateral otic recess, which has been already referred to, and which contains the structures entering into the formation of the middle ear.

In the cranial area of the ventral surface there appears, projecting forward from the ventral surface of the superior utriculoampullary prominence, a distinct, almost vertical, ridge (figs. 5 and 6), which lies immediately medial to the body of the malleus, but is separated therefrom by a sheet of connective tissue. This represents the medial part of the cartilaginous tegmen tympani, or processus perioticus superior. The lateral portion of the tegmen, such as is shown in Voit's model of the skull of lepus, is not present, but its position is indicated by a low ridge, which arches downward and outward from the upper end of the medial portion of the tegmen and marks off the ventral from the lateral surface, terminating below in the crista parotica (fig. 6). The cartilage is not developing rapidly in this location, as in Voit's specimen. Upon examining the model of Hertwig it is found that the tegmen tympani has grown forward and outward to overlie partially the bodies of the malleus and incus, but the lateral portion has evidently made no further development, and so it may be concluded that the ossicles in man do not occupy a deep cartilaginous recess formed by the teg-

men tympani as they do in the rabbit. In the oldest rabbit skull examined by Voit the lateral portion of the tegmen had become quite a prominent plate, covering the ossicles, and reaching out toward the lateral wall of the middle cranial fossa. It appears evident that the tegmen tympani is rudimentary in man.

The crista parotica (figs. 2, 3 and 6) forms a conspicuous object upon the border between the ventral and lateral surfaces. It is narrower, as well as more prominent, below than above, and its edge shows younger cartilage than the adjacent regions. The cartilage of the incus, though in the model it appears to be attached, is really quite separate from that of the ear capsule, there being an intervening sheet of perichondrium.

The lowermost part of the ventral surface lies in a somewhat more posterior plane than the upper, and forms the dorsal wall of a small recess, open in front and below, bounded laterally by the crista parotica and medially by the interfenestral septum of the vestibular portion of the pars cochlearis (or promontorium). In the upper and medial part of this recess appears the lower portion of the fenestra vestibuli, while in the lateral portion, sheltered by the lower part of the crista, the facial nerve is to be found, this region becoming later the lower part of the facial canal or aqueduct of Fallopius. The proximal end of the cartilage of Reichert may be seen just medial to the lower extremity of the crista (fig. 2).

Just below the crista, and separated from it by a small notch, there appears, on the right side, a short, free, anteriorly projecting conical spur of cartilage, slightly younger in character than that of the adjacent otic capsule, and representing the mastoid process of the adult condition (fig. 6). Its substance is directly continuous with that of the ear capsule dorsally, but medially it is separated therefrom by perichondrium. On the left side the same formation is to be seen, except that a portion of the intervening sheet of perichondrium is, near the point of the process, replaced by cartilage. Immediately medial to each process is to be seen the origin of the stapedius muscle.

A brief word as to the course of the facial nerve may here be in place. After entering the internal acoustic meatus it traverses

the facial foramen in a direction outward and slightly forward and enters the ventro-lateral otic recess. Here it becomes associated with the geniculate ganglion from which the great superficial petrosal nerve may be followed forward. Leaving the geniculate ganglion the facial nerve now passes downward and slightly outward over the large cartilaginous bar which unites the pars cochlearis with the pars canalicularis and which is found between the facial foramen above and the vestibular fenestra below; thence it proceeds backward over the incudo-stapedial articulation. It now is to be found just medial to the crista parotica, and runs steeply downward, the relatively small stapedial muscle lying medial to it here. Passing lateral to the upturned end of the cartilage of Reichert, just between the latter and the lower tip of the crista parotica, it gives off the chorda tympani, and turns suddenly forward, following the line of the shaft of Reichert's cartilage, being situated slightly above and lateral to it, and almost immediately lateral to the auditory or Eustachian tube. The relations of the facial nerve at the proximal end of Reichert's cartilage are those shown in Low's ('09) plate, figure 3. The chorda follows its wellknown course through the middle ear anlage.

It is to be noted that the facial nerve does not go through a secondary facial foramen formed by the connection of the tegmen tympani ventrally with the cochlea, as is the case in the rabbit (Voit), and hence there is no true fovea genicularis in the skull of man in this stage, or, indeed, in any stage, judging from the evidence at hand.

The slightly younger condition of the cartilage along the ventral margin of the crista parotica would seem to indicate that the facial canal was closing here, but in the Hertwig model it is still open at this region.

The walls of the pars canalicularis are for the most part thin, and composed of mature cartilage. The largest mass of cartilage is formed by the massa angularis, mentioned above, the ventro-median side of which lies immediately lateral to the fossa subarcuata anterior, while the dorso-lateral side projects outward as the lateral otic eminence. Within the mass, just below the

floor of the anterior subarcuate fossa, there is a small isolated cavity, and as this is within the arch of the anterior semicircular canal I regard it as a remnant of a portion of the otocyst, which is, as yet, unclosed here. The ground substance of the cartilage of this mass is abundant and pale staining, the nuclei being relatively scattered, and surrounded by capsules not increased in size.

The remainder of the cartilage of the pars canalicularis is made up of masses filling the interstices between the canals and ampullae.

The pars cochlearis is the anterior and smaller part of the otic capsule, and lies immediately lateral to the upper end of the basal plate (figs. 1 and 2). Like the pars canalicularis it is of flattened, ovoid form, and contains the sacculus and ductus cochlearis. Upon it we may recognize two principal surfaces, medial and lateral, to which may be added a third or caudal surface, made up of the structures in the vestibular portion surrounding the foramen perilymphaticum.

The medial and lateral surfaces are separated by a rounded border, which runs from the perilymphatic foramen below, around the ventral part of the pars cochlearis, over the cranial pole, and thence backward to terminate by passing over the suprafacial commissure to become continuous with the pars canalicularis at the superior otic notch. The lowermost part of this border is deflected outward to form the promontory; within it is the first and uncoiled part of the cochlear duct, and it is known as the prominentia cochlearis inferior (Voit) (figs. 2, 6 and 7). This prominence passes at first inward, forward and upward, then almost directly upward to reach the cranial pole, and finally passes backward into the prominentia cochlearis superior (Voit) (figs. 1, 6 and 7) as the cranialmost border of the pars cochlearis, which roofs the coiled part of the cochlea (fig. 8), is called. Above the cranial pole the cartilago supracochlearis appears (fig. 3).

The lateral surface of the pars cochlearis (fig. 6) is smooth and gently convex in its ventral portion, and here presents a shallow groove, lying between the promontory and the cranial pole,

though it falls a little short of reaching either of these extremities (fig. 6). It is known as the sulcus caroticus (Voit) and contains a portion of the internal carotid artery (fig. 13). The sulcus caroticus does not correspond to the line of attachment of the lamina spiralis within, but crosses its cranio-ventral convex portion. Its lower part forms a low rounded projection into the lumen of the uncoiled portion of the cochlear duct, which appears in the figure of the cast of the cavity (fig. 8) as a shallow fossa.

The dorsal part of the lateral surface is made up principally by the outer wall of the vestibular portion, and forms the medial wall of the ventro-lateral otic recess. Above, the outlet of the facial foramen is to be seen, bridged by the suprafacial commissure. Below this opening is a small groove, the sulcus facialis (Voit), for the facial nerve, and below this, again, appears the elongated, crescentic, fenestra vestibuli, lying in a general direction from above downward and backward, and presenting a concavity downward and forward. It contains the anlage of the footplate of the stapes, which, however, fills only a small portion of the space of the fenestra, the remainder being occupied by the connective tissue representative of the annular ligament of the base of the stapes. Below the fenestra vestibuli is the cartilaginous septum which separates it from the fenestra perilymphatica below. This septum, which acts as a commissure to join the promontory of the pars cochlearis with the ventral surface of the pars canalicularis, has been referred to by Voit as the promontorium (fig. 6).

Passing below the lower, downwardly concave, border of the promontorium we come upon the small caudal surface of the vestibular portion (fig. 2), marked centrally by the large fenestra perilymphatica, which will later be separated by the processus interperilymphaticus into the larger lateral fenestra cochlearis or rotunda (over which is stretched the membranous anlage of the membrana tympani secondaria), and the smaller, medial foramen for the aquaeductus cochleae, within which may by seen the saccus perilymphaticus (Voit). The interperilymphatic process, more prominent on the left side than on the right, has been referred to, and appears as a short, conical

projection directed forward from the inferior utriculoampullary prominence. The cochlear fenestra is apparently closed off on the left side of the Hertwig model, and almost so on the right.

The perilymphatic fenestra (fig. 2) is sharply concave, from before backward, the direction of the concavity being downward. Its inner wall is formed by the lower edge of the *massa pyramidalis* of the median wall of the vestibular portion. When regarded from below the circumference of the perilymphatic fenestra appears to have been formed by the bifurcation of the inferior cochlear prominence at the promontory, the lateral limb forming the promontorium; the medial the lower border of the massa pyramidalis; the two limbs uniting dorsally in the inter-perilymphatic process.

The boundaries of the medial surface have already been noted (fig. 7). It is quite smooth, and is more flattened than the lateral. Ventrally the elongated, narrow, crescentic line of union with the basal plate may be seen; immediately ventral to and parallel with this, the everted, narrow, extra-cranial surface, formed by the medial aspect of the inferior cochlear prominence, makes up the outer wall of the ventral basicochlear groove (fig. 2) as a strip 1.5 mm. wide.

Dorsal to the basal lamina the medial surface is intracranial, the strip immediately bordering the lamina being concerned in the formation of the outer wall of the dorsal basicochlear groove (fig. 5), which is sharply marked throughout, but more so above than below, In the dorso-cranial area of the medial surface the large, deep, meatus acusticus internus appears (fig. 7); below, the surface passes into the caudal surface of the pars cochlearis and behind into the medial surface of the pars canalicularis.

If we now consider, briefly, the passageway of the ductus cochlearis (figs. 8 and 9) we find the first, or uncoiled part, outwardly deflected at and for a short distance beyond its entrance from the perilymphatic fenestra. The lateral wall is here quite thin, but the opposite medial wall presents a pronounced conical thickening, to which reference has been made as the massa pyramidalis (fig. 2). The apex of the pyramid projects laterally into the first portion

of the cochlear duct, and, indeed, it is owing to this circumstance that this part of the duct is thrust outward to form the promontory on the outer surface. From a point just ventro-cranial to the tip of this pyramid a small commissure, known as the *commissura laminopyramidalis* (fig. 8), springs to join the lamina spiralis which is immediately ventral, and this commissure passes over the uncoiled part of the cochlear duct; at the same time it divides the *crescentic fissure* in the floor of the internal acoustic meatus into ventral and cranial parts. The caudo-ventral surface of the pyramidal mass forms the medial wall of the first part of the cochlear duct; the cranio-ventral surface constitutes the medial and steepest part of the floor of the internal acoustic meatus, while the border between these delimits laterally the slit-like foramen, piercing the ventralmost part of the meatus, which transmits the cochlear division of the acoustic nerve. Dorsally the base of the pyramid is seen to be pierced from above downward and backward by the foramen singulare (fig. 9), which leads into the cavity of the ampulla of the posterior semicircular canal, the region of exit appearing as an indentation of the inner wall just medial to the inner edge of the fenestra perilymphatica. It appears in the cast of the cavity of the capsule as a projection (fig. 9). A small portion of the dorsal side of the pyramid is concerned in the formation of the ventral wall of the vestibular space; the remainder, together with its border joining the cranio-ventral surface, is directly continuous with the cartilage of the medial wall of the vestibular part of the pars cochlearis.

The ductus cochlearis, shortly after passing the level of the lamino-pyramidal commissure (fig. 8), emerges from the vestibular part of the pars cochlearis, and enters the ventral, completely enclosed pars cochlearis (sensu stricto) which contains its coiled part. The only entrances into the closed portion of the cochlea are the passageways for the cochlear duct and the cochlear root of the acoustic nerve. The medial wall is here quite thin, while the lateral wall presents the coiled lamina spiralis (fig. 5).

If the suprafacial commissure were removed (fig. 7) it would be seen that the superior cochlear prominence is continued downward and backward as the first and widest part of the spiral lamina, which here separates the upper coiled portion of the cochlear duct, in front, from the internal acoustic meatus behind. In front of the upper part of the ventro-medial edge of the lamina spiralis, at a point marked by the widened cranio-ventral extremity of the foramen for the cochlear root, the medial downward continuation of the superior cochlear prominence passes over upon the medial surface of the pars cochlearis. When the medial wall of the pars cochlearis is removed it is seen that the lamina spiralis is attached to the lateral wall of the pars cochlearis, the line of attachment being in the form of a helix, which makes but little more than one turn. If the lower edge of the internal acoustic meatus (figs. 5 and 7) be followed forward and inward it passes over the upper edge of the foramen for the cochlear root to reach the medial edge of the lamina spiralis; thence it may be followed along the edge of the narrowing lamina, whose curvature becomes progressively sharper, ending on the lateral wall in a downward turn. In this way there is formed a commodious recess for the upper coiled part of the cochlear duct and its surrounding space. In all the cochlear duct makes about two turns (fig. 8).

The internal acoustic meatus (figs. 5 and 7) presents a rounded border, although its edges are somewhat straightened below and behind. The dorsal portion of the upper border is sharp, and represents the medial edge of the foramen faciale. Passing caudally the edge becomes less sharply marked on the dorsal side, the cartilaginous surfaces which form it here meeting at a right angle. Ventrally we come upon the caudal edge, which is very sharp indeed, and represents the upper edge of the base of the massa pyramidalis. The dorsal and caudal edges form a rounded angle, and about 1 cm. below this point the entrance of the foramen singulare appears. Passing upward from the ventral end of the lower edge we come upon a crescentic and illdefined border which delimits the meatus cranio-ventrally,

and passes dorsally into the medial edge of the suprafacial commissure.

The floor of the meatus is composed of three distinct portions; the ventral, formed by the first part of the lamina spiralis, the dorsal, which is the ventral edge of the wall of the vestibular portion in this region, and the medial, formed by the cranio-ventral surface of the pyramid, as we have seen. These surfaces increase in steepness in the order mentioned, so that the crescentic fissure (fig. 7) formed by their approximated deep edges, is deeper caudo-ventrally than cranio-dorsally. Looked at from within the ventral and dorsal are the only surfaces visible, the ventral presenting much the greater area. The borders of the latter where they join with the margins of the meatus present the enlarged extremities of the crescentic fissure, the upper of which serves for the passage of the facial nerve, the lower and anterior for the upper part of the cochlear division of the acoustic nerve.

Five foramina appear in the internal acoustic meatus, and of these the foramen singulare has been considered. It transmits the posterior ampullary nerve to the inferior cribriform macula. The other four are parts of the crescentic fissure. This latter is divided into almost equal limbs by the lamino-pyramidal commissure, which has been noted overlying the first part of the cochlea, and joining the dorsal surface of the first part of the spiral lamina with the pyramid. The ventral limb is long and slit-like, widest in its ventro-cranial end, and transmits the fibres of the cochlear root of the acoustic nerve. It will later become the spiral foraminous tract. The cranial limb is separated by two cartilaginous septa into three foramina, the upper, which we have seen, being large, and transmitting the 7th cranial nerve, and being known as the facial foramen, the lower two being of about the same size, and transmitting the superior and inferior branches of the vestibular root of the acoustic nerve (figs. 5 and 7).

I have also reconstructed a model of the cavity of the otic capsule, and from the illustrations of this a conception of the general plan of the cavity may be gained (figs. 8 and 9). This

cast includes not only the membranous labyrinth but the space surrounding it, together with the entrances of the various foramina. In the illustration the laminopyramidal commissure appears as a foramen behind the coiled portion of the cochlear tract. In general form the cast resembles the later osseous labyrinth.

The cartilago supracochlearis (figs. 1, 3, 13) may now be considered. This is a small, rounded mass of cartilage, situated upon the cranial pole of the pars cochlearis, and, in the model, is about 8 mm. wide, and almost as long dorso-ventrally. It is quite free from cartilaginous union with the underlying cochlea, but the two are more closely approximated posteriorly than anteriorly, where the intervening connective tissue is thicker. The cartilage is immediately beneath the anterior part of the semilunar ganglion (fig. 13), and the material of which it is formed is mature cartilage of apparently the same age as that in the adjoining pars cochlearis.

It is difficult to say what may be the significance of this cartilage. Certainly it cannot be any one of the Restknorpeln which Voit describes in his Stage II (43 mm.) of the rabbit, since only one of these, Restknorpel b, corresponds at all in position with this cartilage, but it is distinctly above the semilunar ganglion while the supracochlear cartilage is below it. I am inclined to regard it as a rudiment of the commissura (or trabecula) alicochlearis, which Jacoby describes in his 30 mm. human embryo as a cartilaginous bridge extending between the anterior part of the pars cochlearis of the otic capsule and the ala temporalis. There is no evidence in my model of such a commissure, though the surfaces of the processus alaris of the temporal wing and the ventral surface of the pars cochlearis are very close together, and in the later stage modelled by Hertwig (80 mm.) there is no evidence of either commissure or rudimentary cartilage in this location, indicating that the cartilage in my embryo is probably undergoing retrogression. Voit describes and figures such a commissure in the skull of the rabbit, which encloses the carotid foramen laterally. He states it is a direct forward continuation of the planum supracochleare of the pars cochlearis.

The parietal plate (fig. 3) is a thin, semi-crescentic plate of cartilage, situated above and behind the pars canalicularis of the otic capsule, and bearing upon its median surface a concave impression for the brain (fig. 5). The ventral extremity is wide, and is surmounted by an irregularly formed and rudimentary portion, the upper border of which is overlaid laterally by the caudal edge of the parietal bone. Above this part, and lying in the membrane within the parietal bone is to be seen, on the right side, an elongated nodule of cartilage, which may be known as the *cartilago cranii lateralis* (fig. 3)—probably a remnant of the side wall in this region. On the left side there is a somewhat smaller nodule. That this portion is undergoing retrogression is evident from a comprison with the models of Levi, on the one hand, and with the model of Hertwig on the other, when it is seen that the 14 mm. stage of Levi marks, perhaps, the stage of greatest development of the parietal plate, there being, after this, a progressive reduction, moderate in the 28 mm. stage of Levi and in my model, and pronounced in that of Hertwig.

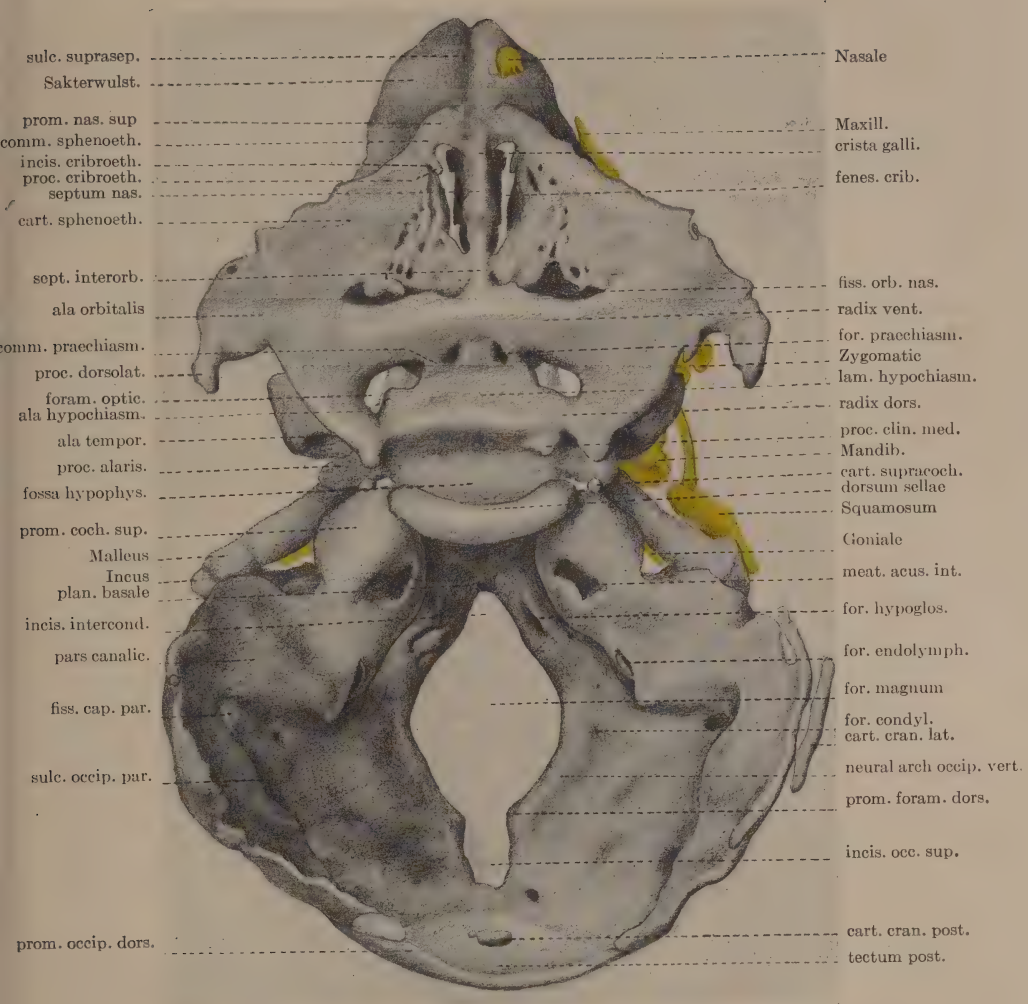
With the otic capsule the parietal plate is connected at two points—in front through the capsuloparietal commissure, and below this through the bridge of cartilage between the capsuloparietal and capsulooccipital fissures. The ventral edge is indented and presents no evidence of the spheno-parietal commissure, such as exists in certain of the lower mammals, as the rabbit and pig, and which represents, according to Gaupp ('00) the taenia marginalis of reptiles. The upper border is concave upward, and in its ventral portion there may be seen a small incisure, open behind, formed by an overhanging, backwardly projecting spicule from the uppermost part of the plate. This incisure appears to be the representative of what Mead calls the fissura laminae parietalis in the skull of Sus, where it is quite conspicuous. The upper border is continuous above with the membrane covering the brain.

The lower border is continuous ventrally with the otic capsule at the upper edge of the capsulooccipital fissure. Behind this it follows the elongated occipitoparietal groove (figs. 1 and 5) which runs backward to the dorsal occipital prominence, and

marks the zone of union with the squama. Several small blood-vessels are found in the ventral portion of the occipitoparietal groove, but in its dorsal part there is but a single small vessel. Just above the groove, and running parallel with it, is a low rounded ridge. The dorsal, scimitar-like extremity of the parietal plate is shown projecting freely dorso-medially. The outer surface is convex and is but indistinctly marked off from the underlying squama.

In the membrane forming the posterior and superior part of the cranium, considerably above the tectum posterius, are to be seen two small cartilages lying side by side, the cartilagines cranii posteriores. The cartilage on the right side, though small, is relatively very large when compared with its partner of the left, which is insignificant.

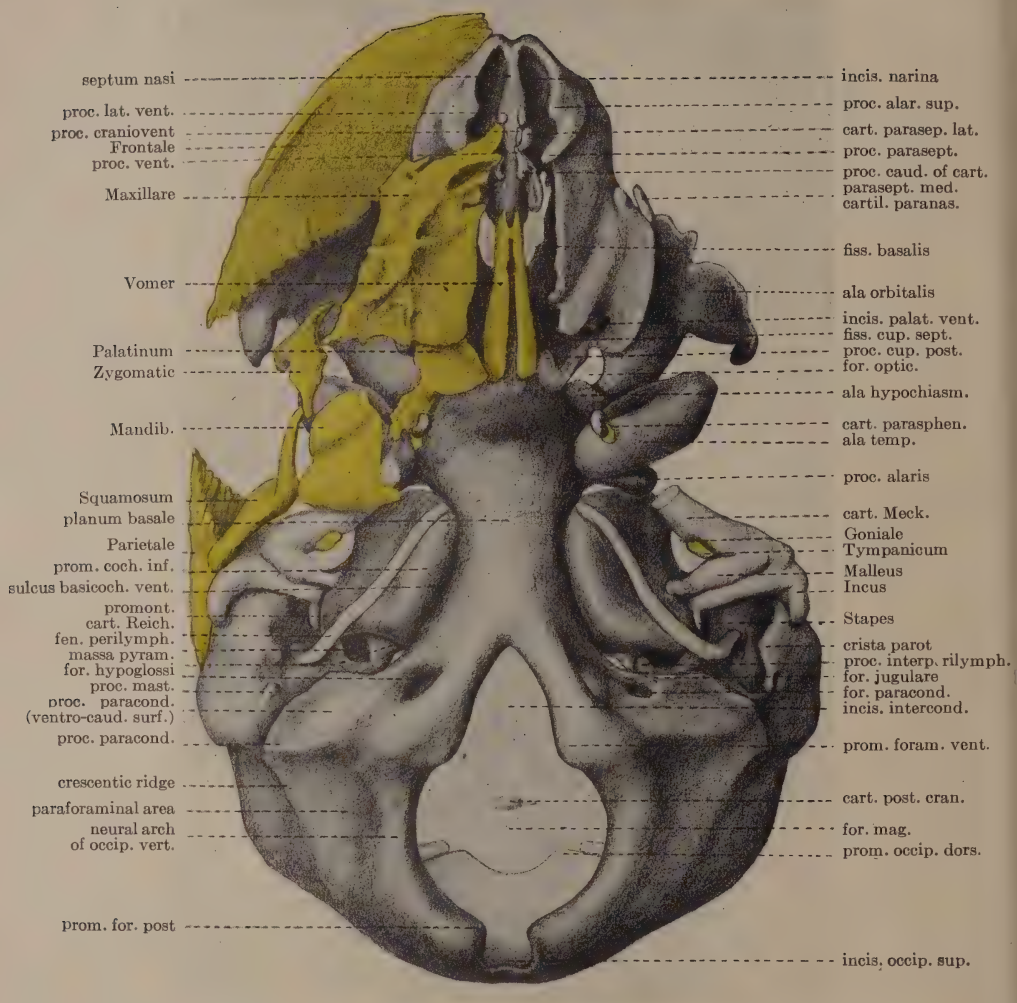
These cartilages appear to represent the unpaired mass described by Bolk as lying above the tectum synoticum, which subsequently disappears. Possibly in my embryo they are undergoing reduction. Mead describes a somewhat similar small free nodule in Sus, but this is single and, although in the midline, it lies immediately above the tectum. He calls it the processus ascendens of the tectum posterius, and thinks it may possibly be the homologue of the processus ascendens of the tectum posterius of reptiles.



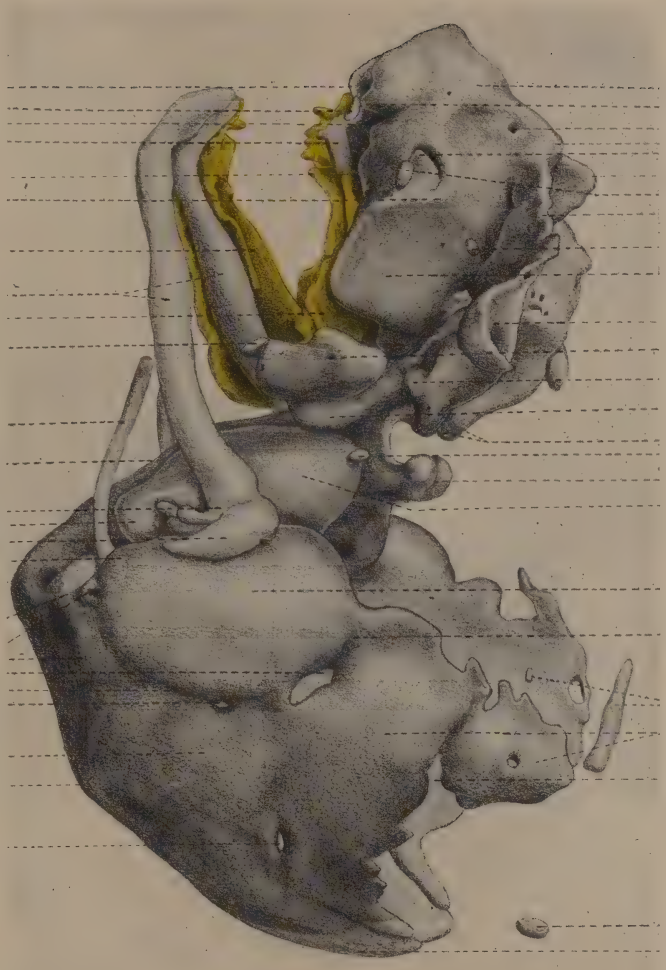
1 Wax plate reconstruction of the chondrocranium of a 40 mm. human fetus, seen from above.

SKULL OF A HUMAN FETUS

CHARLES CLIFFORD MACKLIN



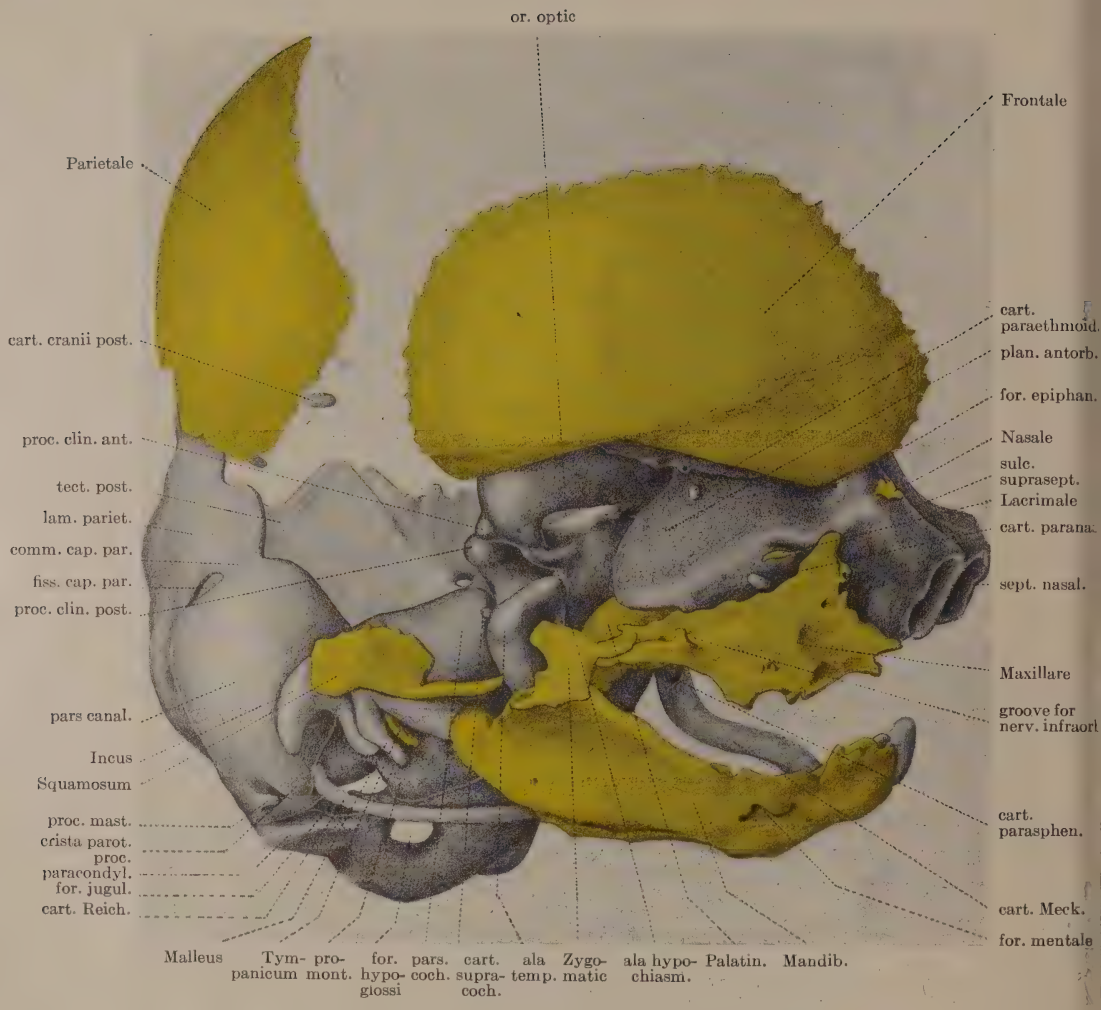
2 Skull seen from below.



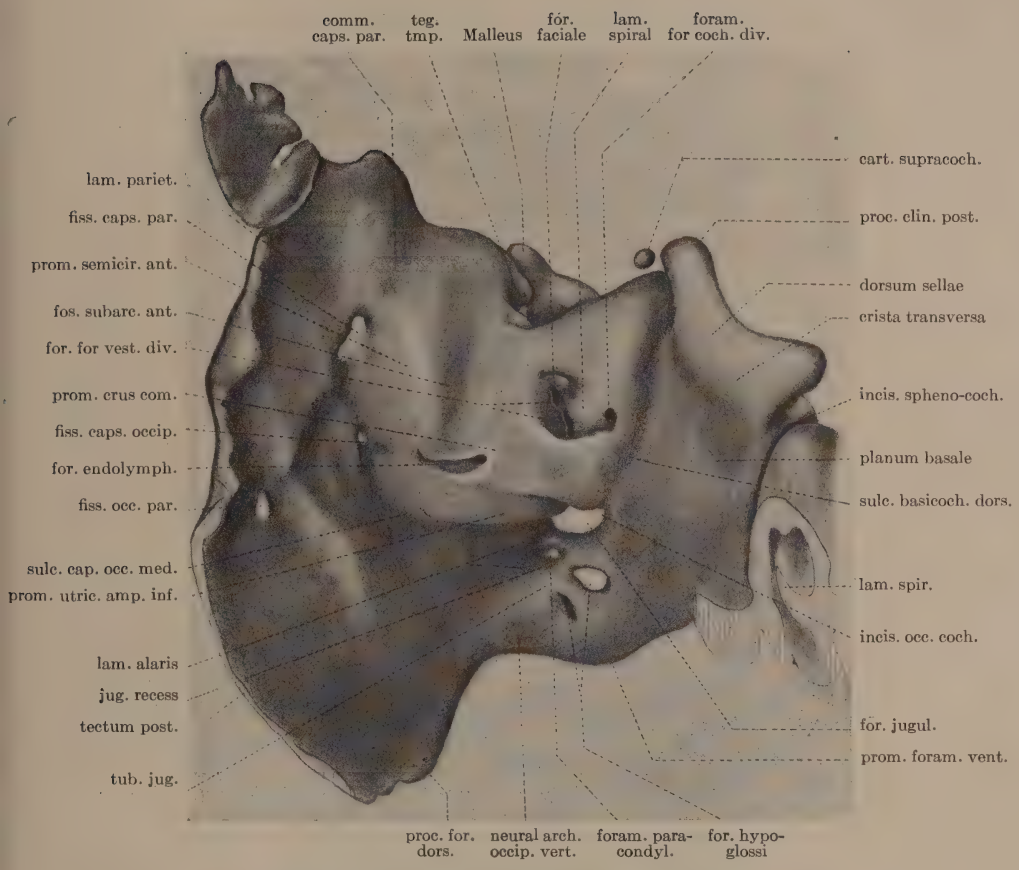
3 Skull seen from left side.

SKULL OF A HUMAN FETUS

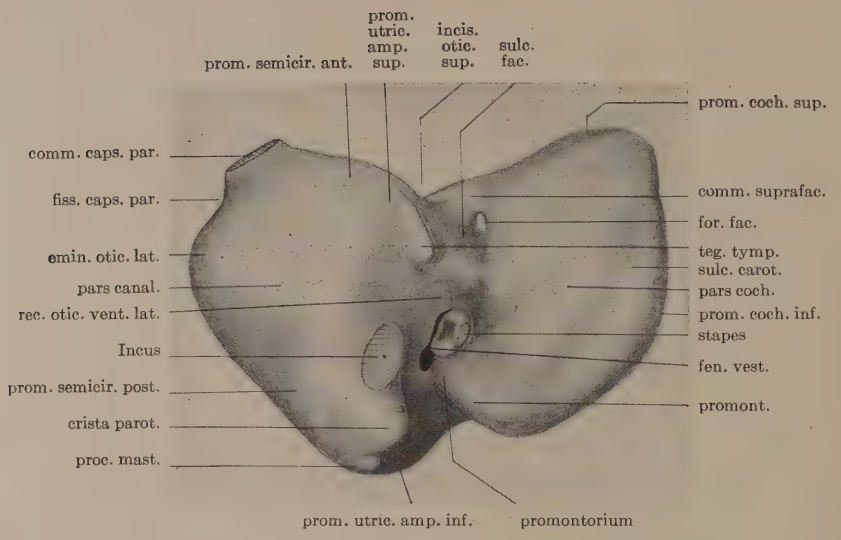
CHARLES CLIFFORD MACKLIN



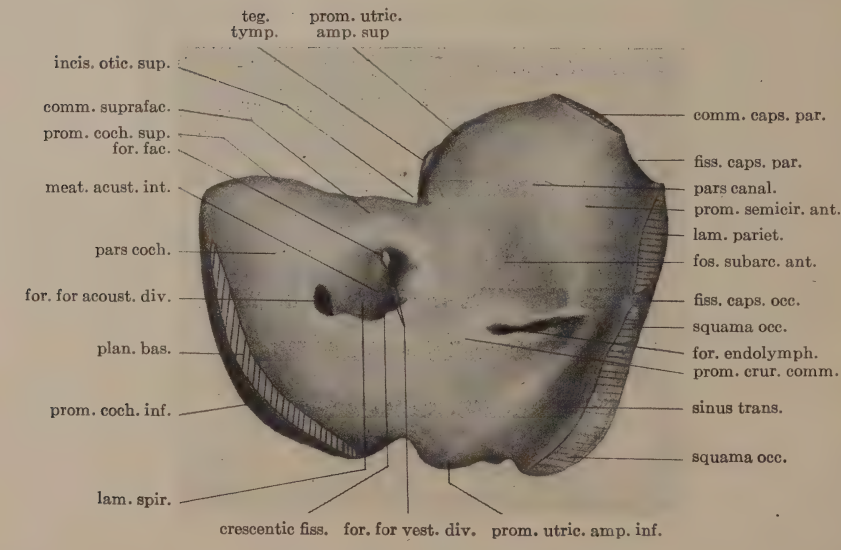
4 Skull showing the right anterior aspect.



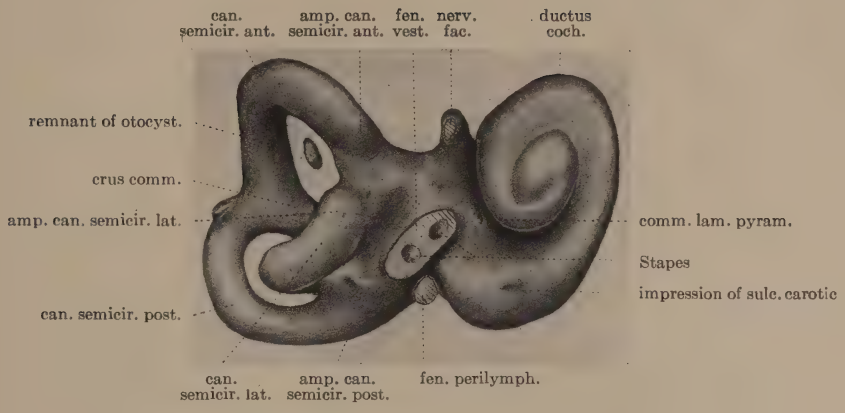
5 The left otic and occipital regions, viewed from within.



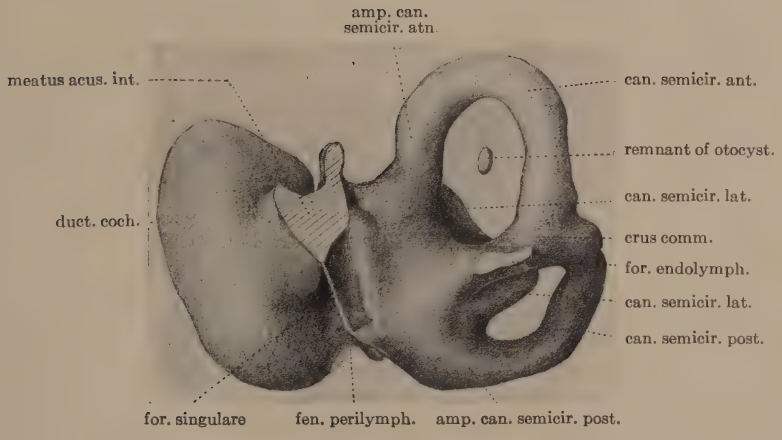
6 Lateral aspect of right otic capsule.



7 Medial aspect of right otic capsule.



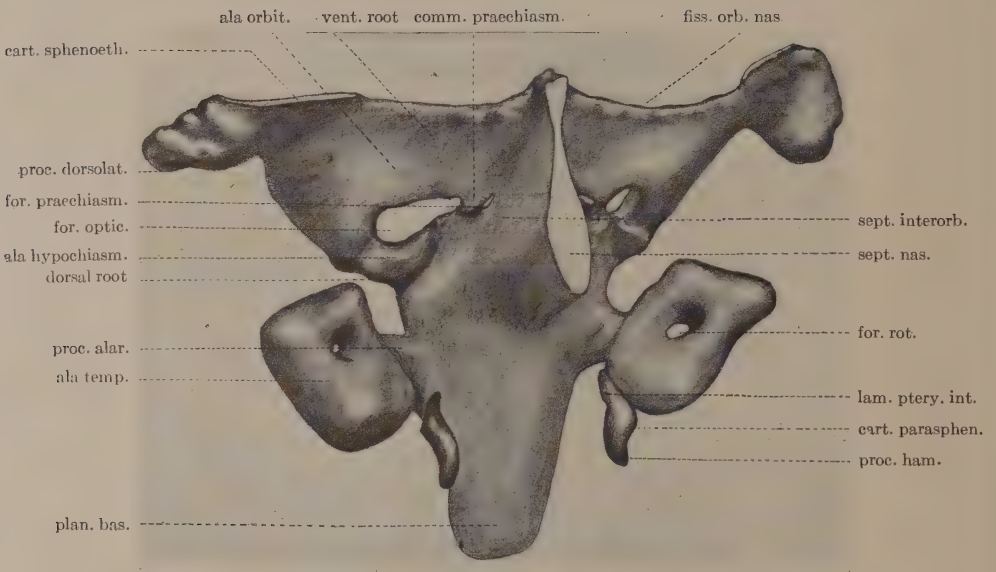
8 Lateral aspect of cast of cavity of the right otic capsule.



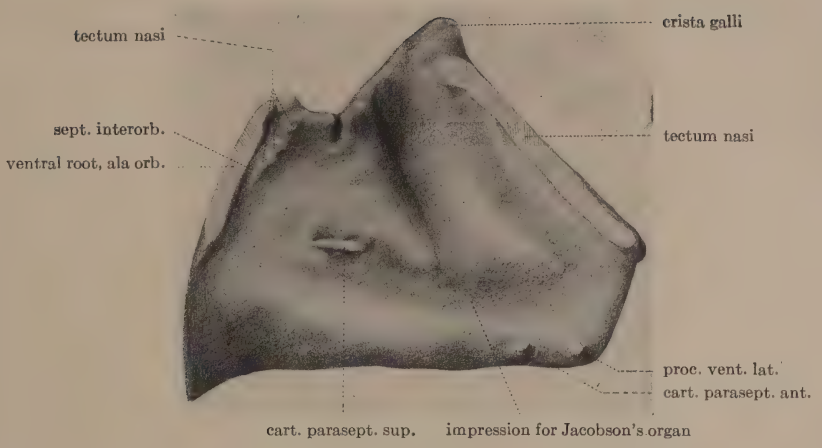
9 Medial aspect of cast of cavity of the right otic capsule.

SKULL OF A HUMAN FETUS

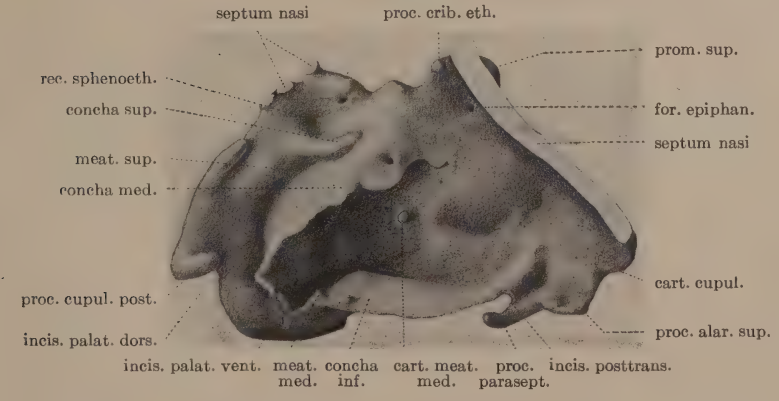
CHARLES CLIFFORD MACKLIN



10 Antero-lateral aspect of detached sphenoidal region.



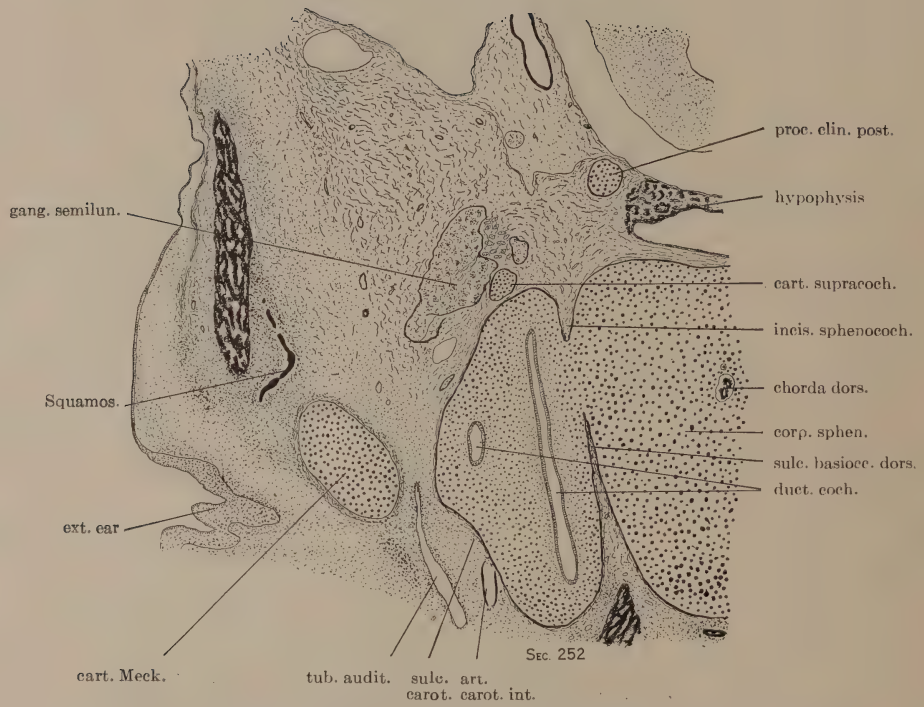
11 Shows the nasal and interorbital septa from the right side. Unions with ventral root of ala orbitalis, tectum nasi of ectethmoid, ventro-lateral process, and anterior paraseptal cartilage are seen. The superior paraseptal cartilage appears in the more dorsal area. The dorsal cut surface of the interorbital septum could not be represented from this position, but it begins above a little below the level of the lower edge of the ventral root of the ala orbitalis. Dorsal to this root the posterior edge of the illustration represents the dorso-cranial border of the septum interorbitalis.



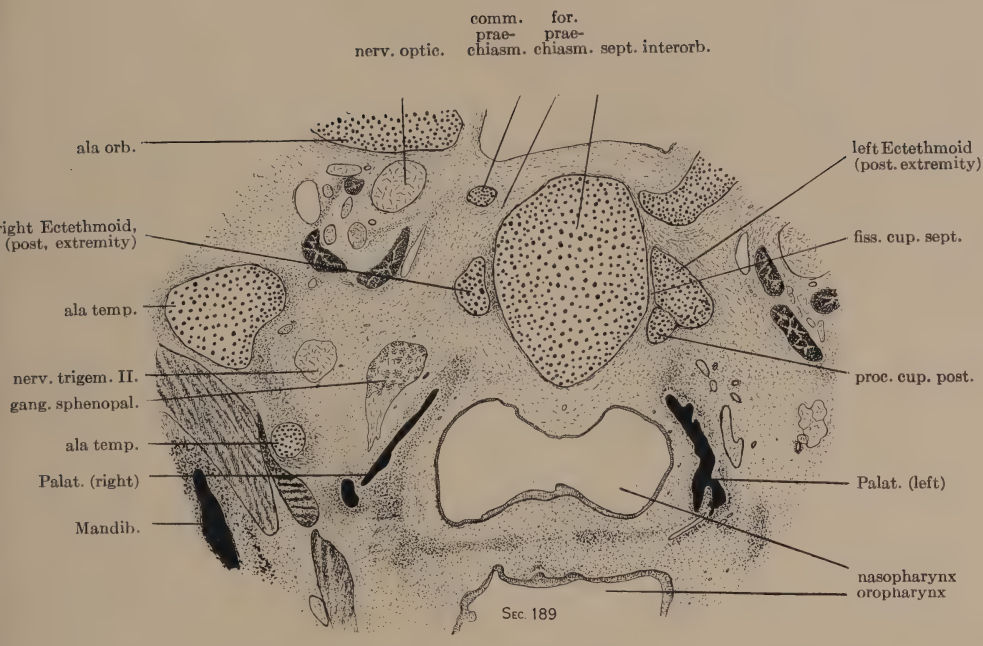
12 Medial aspect of left ectethmoid. Unions with the nasal septum are shown.

SKULL OF A HUMAN FETUS

CHARLES CLIFFORD MACKLIN



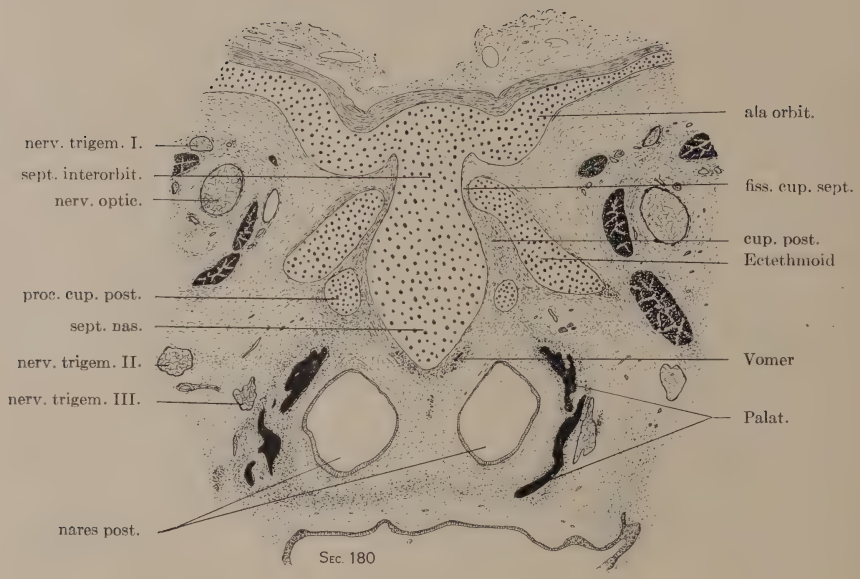
13 Coronal section through head at level of hypophyseal fossa, showing the cartilago supracochlearis overlaid by the semilunar ganglion.



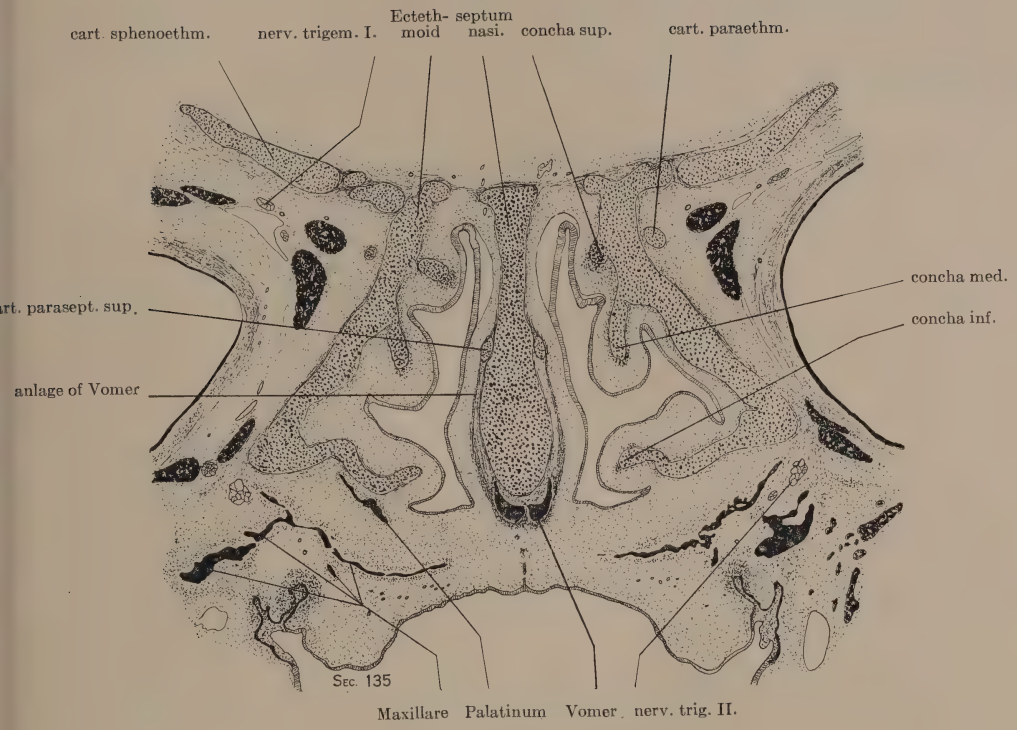
14 Coronal section through head showing dorsal part of ethmoidal and ventral part of orbitotemporal region. Asymmetry is due to obliquity of section. The posterior cupular process on the left side (right side of illustration) is shown joining with the side wall; on the other side, in which the plane of section is posterior, the process is completely joined to the ectethmoid.

SKULL OF A HUMAN FETUS

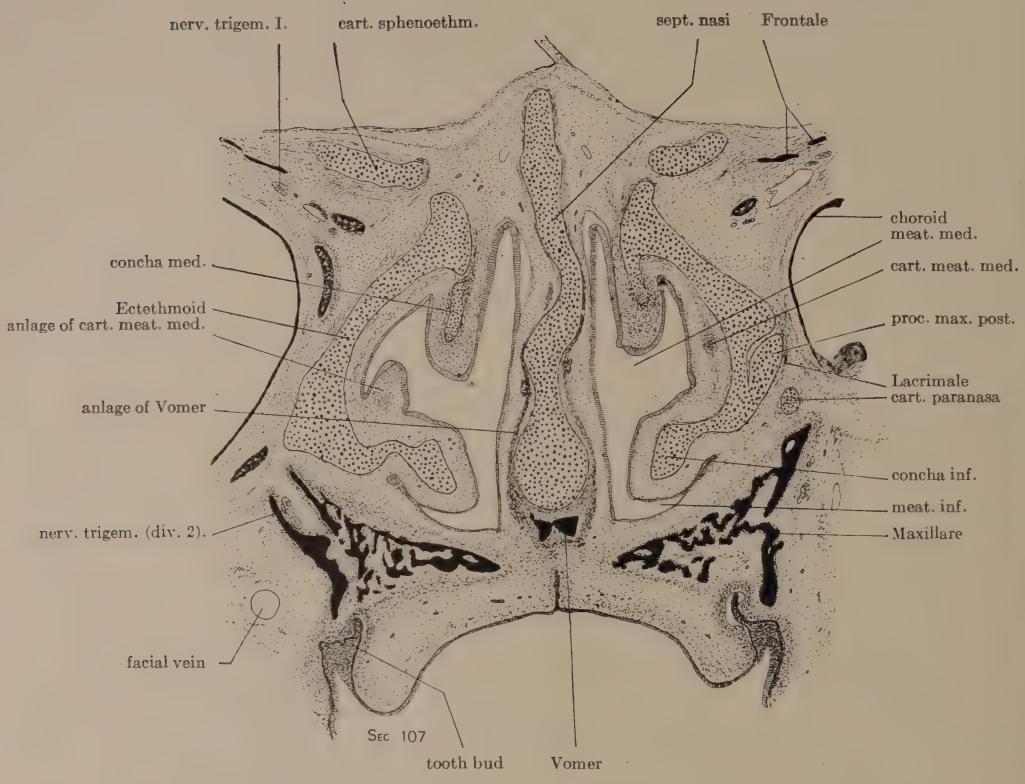
CHARLES CLIFFORD MACKLIN



15 Coronal section through the dorsal part of ethmoidal region, showing posterior cupular process, the nasal septum, the interorbital septum with attached alae, and the palatine and vomer.

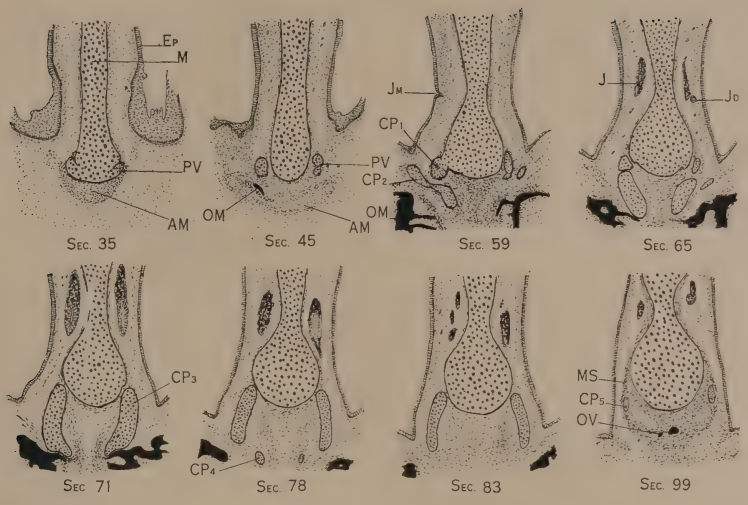


16 Coronal section through the ethmoidal region, showing superior paraseptal cartilages, paraethmoidal cartilages, the vomer, maxilla, and palate bones.



17 Coronal section through ethmoidal region, showing nasal septum, ectethmoid, with attached conchae, cartilago paranasalis, and vomer, maxilla and lacrimal bones.

AM—Anlage of the maxilla
CP_1—Cranio-ventral process of medial lamina of anterior Jacobsonian cartilage
CP_2—Lateral lamina of anterior Jacobsonian cartilage
CP_3—Body of medial lamina of anterior Jacobsonian cartilage
CP_4—Caudal process of medial lamina of anterior Jacobsonian cartilage
CP_5—Dorsal extremity of lamina of medial anterior Jacobsonian cartilage
Ep—Epithelium of nasal cavity
J—Organ of Jacobson (right)
Jd—Duct of left organ of Jacobson
Jm—Meatus of duct of right organ of Jacobson
M—Mesethmoid
MS—"Suspensory membrane" of Fawcett, the anlage of the vomer
OM—Maxilla
OV—Vomer
PV—Ventro-lateral process



18 Series of eight coronal cross-sections, through caudal portion of mesethmoid, in the region of the anterior paraseptal cartilages. Sections numbers 35, 45, 59, 65, 71, 78, 83, and 99. Magnif.

Section 35 shows the ventral end of the ventro-lateral process, *PV*, and its connection with the caudal border of the mesethmoid. In section 45 the dorsal ends of these processes are shown in cross section, with the ventral extremity of the maxilla *OM*; the membranous anlage of this bone appears in sections 35 and 45—*AM*. Part of the epithelium of the nasal cavity is represented in all the sections *Ep*. Section 59 is through the ventral end of Jacobson's cartilage and shows the cranio-ventral process of the medial lamina CP_1 on the right side attached to the mesethmoid, while the outer lamina, CP_2 lies free in the mesenchyme. Owing to the section having been cut somewhat more deeply on the right than on the left side, the left side of the illustration shows a somewhat more dorsal plane than does the right. The meatus of the right Jacobsonian duct opens at *Jm* in section 59. Section 65 shows, on the right side, the dorsal tip of the left outer lamina of Jacobson's cartilage, and medial to this the main part of the inner lamina below, and the cranio-ventral process above. The organ of Jacobson appears in this and following sections, and it will be observed that the mesethmoid has become quite thin in its vicinity, the organ lying in a concavity of the cartilage. In section 71 the main lamina of Jacobson's cartilage is seen CP_3, and it will be noted that at its caudal extremity the relationship to the maxilla is very intimate. In the next section, No. 78, the caudal process is seen separated from the main mass of the cartilage, and in the next section, No. 83, this process has disappeared. In No. 99 the dorsal tips of the Jacobsonian cartilages are seen CP_5, and below the mesethmoid, lying in a mass of condensed mesenchyme, the anterior tips of the vomer are seen as two small spicules of bone.

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II. THE SKULL OF A HUMAN FETUS OF 40 MM.[1]

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Regio orbitotemporalis

The orbitotemporal region, in the present stage, is composed of the cartilage of the sphenoidal anlage and unites the otic region, behind, with the ethmoidal region in front. In it we recognize an unpaired, median portion, made up of that part of the central stem of the chondrocranium which contains the bend; this represents principally the cartilaginous body of the sphenoid, and is directly continuous dorsally with the otic portion of the planum basale and ventrally with the nasal septum of the ethmoidal region. In addition there are two paired, lateral parts, the forerunners of the greater and lesser wings. The internal pterygoid plate, which is laid down in membrane bone, will be considered in the section devoted to the discussion of the purely osseous elements.

If we examine, successively, the parts of the median portion, beginning dorsally, we note first a prominent transverse ridge, the crista transversa (fig. 5), which marks the boundary between the orbitotemporal and otic portions of the median stem. Directly continuous with this ridge, and springing upward from it, is the prominent dorsum sellae (figs. 1 and 3), here showing no median perforation, as it does in the rabbit (Voit), and it is owing to this circumstance that the upper edge of the crista is, in homo, entirely obliterated.

The dorsum sellae forms the conspicuous posterior wall of the hypophyseal fossa. Its upper and lateral corners are thickened

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and project upward, outward and forward in a horn-like manner, so that their ventral extremities overlie, to some extent, the hypophyseal fossa. These are the posterior clinoid processes. Their upper extremities rise higher than the cranial edge of the dorsum sellae between them, and hence the latter is concave cranially, as well as ventrally. The dorsal surface of the dorsum sellae is gently concave from side to side, and from above downward, passing uniformly over upon the surface of the otic portion of the planum basale below.

Histologically there is here, at this stage, no evidence of the primary separation of the chondrous anlagen of the dorsum sellae, such as Fawcett describes in earlier stages (19 and 21 mm.), except a slightly younger condition of the cartilage at the ventral side of the junction of the dorsum sellae and crista transversa.

In front of the dorsum sellae we come upon the wide, flattened floor of the hypophyseal fossa (fig. 1), or sella turcica, which opens laterally into the side-parts of the middle cranial fossa, and is thus more correctly a short wide groove than a fossa. Ventrally the wall rises abruptly,—almost vertically,—to reach a transverse ridge,—the anlage of the tuberculum sellae. The lateral edge of the ventral wall presents, on the right side, but not on the left, a small, conical backwardly projecting middle clinoid process. The tuberculum sellae of my model is much more prominent than it is in that of Hertwig. It is interesting to note in passing that Levi is of the opinion that in the development of the human skull the sella turcica is the only part to retain its primitive position, the other parts moving cranially, and he finds in the 28 mm. stage, among other evidences of this, the appearance of the tuberculum sellae as the anterior wall of the sella turcica. There is no evidence of the tuberculum sellae in the 17 mm. stage, while in the 28 mm. stage the sella has a vertical ventral wall, as in my model.

The part of the central stem of the chondrocranium composing the floor and ventral wall of the sella turcica has been termed the Balkenplatte or lamina trabeculi. It is wide, and, when compared with the parts in front and behind it, quite thin. It shows no evidence of perforation. From the ventral half of each

lateral edge of the floor there is seen to project, in a direction downward and outward, the short, rod-like processus alaris.

When the model is regarded from the side (fig. 3), the floor of the sella turcica, which is slightly concave cranially, appears as the upper expanded end of the planum basale, the ventral wall of the sella appearing as a continuation upward of the ventral surface of the planum; indeed if the ventral border of the latter (which we have noted is almost straight) is projected upward it will pass just ventral to, and parallel with, the ventral wall aforementioned. From the same position, too, the ventral wall of the sella appears as the dorsal expanded end of the cranio-ventral or horizontal limb of the central stem of the chondrocranium, and the appearance is as if the caudo-dorsal edge of this had been applied to the cranio-ventral edge of the vertical limb, making an angle of 115°, open caudo-ventrally, the flattened extremities forming the ventral wall and floor of the sella turcica respectively. Ventrally (fig. 2) this angle is seen to be quite sharply marked, and to lie on the line between the ventral edges of the roots of the processus alares, or, just below the level of the ventral wall of the sella. Ventral to this angle the cartilage of the central stem gradually becomes narrower from side to side, and expanded caudo-cranially, passing ventrally into the nasal septum (fig. 10).

If we now turn our attention again to the upper surface of the median stem, we pass forward from the sella turcica, over the rounded, transverse, tuberculum sellae, and come upon the flattened lamina hypochiasmatica (fig. 1) (sulcus chiasmaticus of Levi), triangular in shape, with the apex placed ventrally in the midline, and the base formed by the upper edge of the ventral wall of the sella turcica. This surface underlies the optic chiasma, and is horizontal, thus making almost a right angle with the ventral wall of the sella. Ventrally the apex rises upon the dorsal edge of the interorbital septum, forming therewith an angle of 120°. Immediately lateral to this junction is a small, slit-like foramen, which may be known as the *foramen praechiasmaticum* (figs. 1, 10 and 14); it has been shown in the models of the skulls of several mammals, as the ape (Fischer) and the rabbit (Voit),

as well as man (Hertwig). It contains nothing but loose connective tissue. It does not appear in Jacoby's figure, but the optic foramen extends all the way to the interorbital septum, and one may assume from this that the small isthmus of cartilage, which cuts off this small aperture from the optic foramen, and which may be known as the *commissura praechiasmatica* (figs. 1, 10, 14), has been developed between the 30 and 40 mm. stages. In my sections this commissure shows a rather younger condition of cartilage than that found in the surrounding chondrocranium. The foramen praechiasmaticum evidently disappears later, as it is not to be found in the osseous condition. At the dorsal extremity of the optic foramen the lamina hypochiasmatica is seen to pass over upon the dorsal root of the ala orbitalis.

A feature which I have not noticed in the description of human primitive skulls, but which is described by Voit in the skull of lepus, as the ala hypochiasmatica, is a small but strong crescentic ridge which projects antero-laterally from the surface of the lamina hypochiasmatica just ventral to the origin of the dorsal root of the ala orbitalis, and which is continuous dorsally with this root. It appears in figure 10 and may be seen from above as a projection into the optic foramen (fig. 1). It presents a convex ventral edge, and is separated from the surface of the interorbital septum, lying within, by a distinct furrow containing only connective tissue. In the Voit model of the skull of rabbit this shows beginning ossification, but such is not the case in my model, in which the ala presents a somewhat younger type of cartilage, especially in the ventral edge, when compared with that of the adjacent cartilage.

Ventrally, as we have seen, the lamina hypochiasmatica is continuous, medially, with the dorsal border of the interorbital septum. From the sides of this septum the ventral roots of the alae orbitales are seen to spring (fig. 1), and its cranialmost edge, delimiting the orbitonasal fissure medially, passes over directly upon the nasal septum.

The interorbital septum (figs. 10, 11, 14 and 15) is narrow cranially, being delimited dorsally by the roots of the alae orbi-

tales and ventrally by the dorsal extremities of the side-walls of the ethmoidal region (fig. 11). It is thicker below than above, its lower surface being keel-like, and passing horizontally forward upon the lower edge of the nasal septum; the upper part becoming increasingly thinner as we follow it ventrally, to coalesce with the upper portion of the same structure. It represents a transition from the flattened Balkenplatte to the thin nasal septum, in which the median stem appears to undergo a torsion of 90°, and forms the median delimitation of the narrow inner recess of the orbit.

The interorbital septum of man is homologous with the structure bearing the same name found in the Saurians, but, as is the case in the other mammals, it is rudimentary when compared with these lower forms. A theory which seeks to account for the shortness of this septum when compared with the condition in the lower forms is that, in the mammals, the nasal side-wall has gradually grown backwards, to encroach more and more upon the territory of the interorbital septum, to the advantage of the nasal septum (Mead).

If we start at the floor of the sella turcica (fig. 1), and proceed upward and forward we come upon three successive steps, at about equal intervals apart, formed, as we have seen, by the lamina hypochiasmatica, the uppermost edge of the interorbital septum, and finally, in the most cranial, which reaches the highest point of the chondrocranium, by the crista galli of the mesethmoid (fig. 11).

The orbital wings (figs. 1 and 10) are the cranio-ventral and the larger of the paired lateral extensions of the sphenoidal anlage. Each wing has the form of an imperfectly defined, triangular plate, with the irregular base parallel with the median plane, and the apex lateral and turned dorsally. The plate is gently concave downward, forming the roof of the orbit; above it takes part in the formation of the floor of the anterior cranial fossa. Of the unions, two are with the central stem of the chondrocranium, the dorsal and ventral roots, and one which is elongated and broken by several foramina is with the side-wall of the ethmoidal region. The two wings lie almost hori-

zontally, and thus differ from the earlier conditions, where they are considerably higher laterally than medially (Jacoby).

The dorsal root is the smaller, and is directed outward and slightly upward. Thick and rounded in section, its cartilage is directly continuous with that of the lamina hypochiasmatica, from the side of which it has been seen to project. A short distance from its origin it widens out, and at the same time rises cranially to form a plate, flattened from above downward, outward and slightly forward, the dorsal edge of which presents, near the median line, a backward projection, the anterior clinoid process (fig. 3). Between this process and the edge of the Balkenplatte, rendered more sharply defined on the right side by the middle clinoid process, there is to be seen a distinct notch, which lies dorsal to the root, opposite the most posterior extremity of the optic foramen, and conveys the internal carotid artery. The dorsal border of the wing, after leaving the anterior clinoid process, passes upward, forward and outward, making a dorso-lateral convexity, and finally turns abruptly backward upon the dorso-lateral process. The ventral border of the root forms the dorsal and part of the lateral border of the foramen opticum, while its lower surface, together with that of the wing lateral to it, forms the cranial delimitation of the superior orbital fissure.

The ventral root is wide and flat, and is directed outward and slightly backward. It is considerably the longer, as well as the broader, and is directly attached to the dorsal border of the interorbital septum along the line indicated in figure 11. In addition it is connected, through the praechiasmatic commissure, with the ventro-lateral edge of the hypochiasmatic lamina (fig. 1). The ventral root occupies a somewhat higher level than the dorsal. The dorsal border curves outward and backward, to assist in the delimitation of the foramen opticum; the ventral border passes almost directly outward, and forms the dorsal border of the orbitonasal fissure. Through the portion of the wing lying lateral to the optic foramen it is continuous with the dorsal root; and in this way is formed the shelving side of a recess, the floor of which is made up of the hypochiasmatic

lamina, in which is found, among other structures, the optic chiasma.

The optic foramen is pear-shaped in outline, with the narrow end ventro-medial. The lateral border is somewhat higher than the medial, and is downwardly and inwardly concave. The optic nerve and ophthalmic artery may be seen to pass through it, the former overlying the latter.

The ventralmost portion of the orbital wing has been known by the name of cartilago sphenoethmoidalis. This is a triangular plate of cartilage, somewhat thinner than that composing the remainder of the wing, and showing ventrally a connection with the superior prominence of the lateral nasal cartilage through the sphenoethmoidal commissure (fig. 1), and dorsal to this connections at several points with the lateral nasal cartilage as far back as the orbitonasal fissure, the bonds of attachment being broken by intervening foramina. Thus there is formed here a secondary, lateral cribriform plate, similar to that shown in the model of Hertwig, which leads from the anterior cranial fossa, not into the nasal capsule, but into the orbit. The dorsal margin is irregular and forms the outer half of the ventral margin of the orbitonasal fissure, the medial half being formed by the dorsal surface of the ectethmoid.

The ventral border of the orbitonasal fissure is somewhat lower than the dorsal. The fissure is elongated, its long dimension being directed laterally, and in this it differs from the condition shown in the skull of lepus (Voit), where it is directed ventro-laterally. In the latter animal, too, there are no connections with the ectethmoid dorsal to the sphenoethmoidal commissure. As in the skull of lepus (Voit) so in man, the fissure is principally filled with connective tissue, but in its ventral region it transmits the anterior ethmoidal nerve and vessels from the orbit to the anterior cranial fossa. It is thus, in this region, representative of the anterior ethmoidal foramen of the adult skull.

The lateral border of the ala orbitalis is serrated, and passes directly backward and outward to terminate in the hornlike, dorso-lateral process (fig. 1). It overlies, except at its tip, the

median edge of the orbital plate of the frontal bone (fig. 2). The dorso-lateral process marks the lateral extremity of the ala, and also represents the ventral rudiment of the primitive taenia marginalis of this region, which in the lower forms stretches over the foramen sphenoparietale to make a connection with the parietal plate, as has been already noted.

The ala temporalis (fig. 10) is the smaller of the paired lateral appendages of the median portion of the sphenoidal anlage. It lies lateral to the Balkenplatte, and, for the most part, in front of and below the level of the floor of the sella turcica (fig. 3). As H. Fuchs remarks one must distinguish in the temporal wing of mammals two portions; a medial, sloping steeply downward and outward, and a lateral, ascending part. The medial portion, or processus alaris, is a short, straight, rodlike mass of cartilage, directly continuous with the outer edge of the Balkenplatte, from which, as we have seen, it projects downward, outward and slightly backward. Its dorsal surface comes into close contact with the cranio-ventral pole of the pars cochlearis, but is not connected therewith by a cartilaginous bridge (commissura alicochlearis), as is the case in the Jacoby model, and in the models of several of the lower mammals. What I regard as a remnant of this bridge is, however, to be found in the supracochlear cartilage, which has already been described. Levi was unable to find any trace of this commissure in his specimens.

It may be noted in passing that Jacoby states that this bridge extends from the lateral edge of the sella turcica to the anterior edge of the ear capsule, but he has evidently included in the median portion of this the structure which other authors refer to as the processus alaris. Jacoby states that the ala temporalis springs outward from this bridge; perhaps a better way of stating it would be to say that the ala temporalis, through the processus alaris, springs from the edge of the floor of the hypophyseal fossa, and that the bridge, or commissura alicochlearis, connects the ala with the anterior surface of the pars cochlearis of the otic capsule. By the disappearance of the commissura alicochlearis the carotid foramen is left open laterally. It is quite small, being delimited ventrally by a small notch between

the root of the alar process and the Balkenplatte, and dorsally by the ventral basicochlear groove, which passes backward into the sphenocochlear notch.

The ventral surface of the alar process is almost completely taken up with the attachment of the lateral portion of the wing. The rounded outer extremity projects freely into the surrounding mesenchyme (fig. 1).

The larger lateral portion of the temporal wing lies immediately below the dorsal portion of the orbital wing, from which it is separated by the superior orbital fissure, now open laterally (fig. 4). It is rhomboidal in shape, the long axis being directed upward, outward and slightly forward, towards the lateral extremity of the ala orbitalis. The central portion of its mass is perforated, from before backward, by the large foramen rotundum, which transmits the second branch of the trigeminal nerve. The nerve, however, by no means fills the foramen, the greater portion of the space within it being occupied by connective tissue. The foramen rotundum is found in Levi's 28 mm. stage, but not in Jacoby's 30 mm. stage, the second branch of the fifth nerve here occupying a groove upon the upper surface of the wing. It is well shown in the illustrations of Fischer's ('03) ape skulls.

Immediately below the foramen rotundum the dorsal surface is concerned in the union with the ventral surface of the alar process, the long axes of the medial and lateral portions crossing at a right angle, open above. When regarded from above the effect is as if the caudo-medial corner of the lateral portion had been applied to the ventral surface of the medial portion in such a way as to leave the lower extremities of both free. The foramen ovale is not as yet formed.

Histologically there is to be seen at the junction of the alar process and lateral portion a sheet of younger cartilage and procartilage cells, which almost completely separates the two portions. This is evidently the last trace of the primitive separation of these parts, of which Levi, Fawcett and other authors speak. In the 14 mm. stage Levi finds the temporal wing represented by two procartilaginous anlagen, separated by a sheet of connective tissue.

The portion of the wing above the foramen rotundum is known as the lamina ascendens, and ends laterally in a somewhat sharp angle, which projects freely outward and forward. The uppermost angle, rather more blunt, is to be seen almost immediately under the lateral edge of the optic foramen. The dorsal surface of the lamina ascendens is convex, and terminates dorsally in a ridge, bordering the foramen rotundum laterally.

The lowest portion of the wing is marked by a blunt angle, lying below and a little medial to the foramen rotundum, and representing the processus pterygoideus. The innermost extremity of the wing presents a more sharply marked angle, which projects freely inward, where it comes into close contact with the parasphenoid bone, or internal pterygoid plate, the upper extremity of which lies immediately ventro-medial to it. Medially and caudally this angle is separated from the alar process by a well-marked groove,—the deepest part of the circular groove which surrounds the union of the alar process and the lateral portion.

The outer margin of the lateral portion projects farther forward than the medial (fig. 14) so that its ventral face looks inward as well as forward. There is no trace of a lamina pterygoidea, perforated by the internal maxillary artery, such as Voit describes in the skull of the rabbit.

Histologically, modification of the cartilage cells in the upper lateral portion of the wing indicates beginning endochondral ossification; Mall found the first trace of the alisphenoid bone in an embryo of 58 days. Medial to the foramen rotundum the cartilage is thinner and of younger character than that elsewhere in the lateral portion, indicating that this was the part which was, perhaps, latest to form.

Gaupp has pointed out that the brain-case of the mammals has, in the orbitotemporal region, been enlarged by the inclusion of a space which, in the lizards, lies below the primitive side-wall of this region, and to which he has given the name 'cavum epiptericum.' This space is the ventral continuation of the cavity which has been described by Voit in lepus as the cavum supracochleare. Voit has found in an early rabbit embryo

evidences of the medial attachment of the primitive side-wall of the orbitotemporal region in the form of three rudimentary cartilages, and membrane connecting them, and stretching out from them. From behind forward he finds, first, Restknorpel *a*, surmounting the commissura suprafacialis (continuous with this on one side but not on the other), next Restknorpel *b*, overlying the semilunar ganglion, and connected by a sheet of connective tissue, which overlies the abducens nerve, with the pillar of the dorsum sellae. Restknorpel *b* is quite free. A third rudimentary cartilage, Restknorpel *c*, appears only on the left side of Voit's youngest rabbit skull, and this fact appears to point to its transient nature. It presents itself at about the site apparently of the middle clinoid process, and is attached directly to the side of the Balkenplatte. Between Restknorpeln *b* and *c* the boundary between the primitive cranial cavity and the cavum epiptericum is not clearly marked. From these three Restknorpeln, and from the cartilage intervening, anchorage is afforded for a stout sheet of connective tissue which stretches outward and upward to find its cranial attachment in the lower edge of the taenia marginalis, or, as Voit calls it in this region, the commissura orbitoparietalis. Underlying this membrane, which Voit thinks is, to some extent, the precursor of the dura mater of this region, are several important structures which are primarily outside of the primitive brain case, as in the lizards, but are later taken into the brain case of the mammals; among these have already been mentioned the semilunar ganglion and part of its nerve trunks, part of the facial nerve, the geniculate ganglion and part of the great superficial petrosal nerve. In addition might be mentioned the nerves to the eye muscles, and the internal carotid artery—indeed all the structures in the cavernous sinus. The carotid artery is shown in the youngest stage of Voit winding around the caudo-ventral surface of Restknorpel *c* to enter the primitive cranium, this point marking its original inlet.

From the researches of Voit it would appear that the new floor and side-wall of the cavum epiptericum and the cavum supracochleare are formed by the upper part of the ala temporalis,

the tegmen tympani and its forward extension, and the commissura alicochlearis, together with the osseous elements formed by the parietal, and squamous portion of the temporal, bones. These completely shut off this space, except for the foramina.

In my embryo there do not appear to be any of the nodules corresponding to the three Restknorpeln of Voit. The space corresponding to the above cavities is filled with loose connective tissue containing vessels and nerves. The dura has not condensed, is loose, and spreads outward and upward from the level of the upper part of the pituitary body. Thus the primitive cranial floor and side-wall of this region is not represented in my model. There is, however, what may be a rudiment of the cartilaginous secondary cranial floor—the floor of the cavum epiptericum, viz., the small nodule which I have called the cartilago supracochleare. Voit considers the alicochlearis a part of this floor, which dorsally is directly continuous with the planum supracochleare; this being so it follows that, if the cartilago supracochleare be regarded as a rudiment of the commissura alicochlearis it is then a rudiment of the cartilaginous floor of the cavum epiptericum, or, more accurately, the cavum supracochleare.

Regio ethmoidalis

The ethmoidal region is the most ventral of the primary divisions of the chondrocranium. With the orbitotemporal region it is directly continuous at three points, as we have seen; medially the septum nasi passes directly backward into the septum interorbitale, and laterally the upper portion of the lateral wall of the ectethmoid is united, on each side, with the sphenoethmoidal cartilage through the sphenoethmoidal commissure and the line of bridges of cartilage dorsal to the latter.

Architecturally considered the principal elements entering into the construction of the ethmoidal region are those going to form the nasal capsule, but this region also includes certain accessory cartilages, of which there are, in relation to the septum the anterior and superior paraseptals; in relation to the lateral wall (intracapsular) the cartilago meatus medii, and (extracapsular) the paraethmoidal and paranasal cartilages.

The nasal capsule resembles, roughly, a tent, partitioned into equal, paired, lateral rooms or cavities by the septum, or mesethmoid, which lies in the median sagittal plane of the skull. The highest point, or peak, is marked by the crista galli. The roof and sides are formed by the tectum nasi and paries nasi respectively, the posterior or subcerebral portion of the former being broken by the long, paired, irregularly-contoured fenestrae cribrosae (fig. 1), destined to become the cribriform plate. This portion of the superior surface of the capsule takes part in the formation of the median part of the anterior cranial fossa, and represents the anlage of the upper surface of the ethmoid bone.

The incomplete floor (fig. 2), or solum nasi, is formed laterally by the inwardly-turned lower edges of the side-walls, and medially by the lower border of the septum and the anterior paraseptal cartilages. Between the side-wall and the septum is the gaping and elongated basal fissure, which extends ventrally into the incisura narina and dorsally into the *cupuloseptal fissure*, the latter being a very narrow space between the dorsalmost extremities of the nasal septum and the nasal wall, almost completely filled by perichondrium. The floor is almost entirely covered in by membrane bones—the maxilla, the palatine and the vomer—these closing off the inferior nasal meatus below, and marking the upper delimitation of the oral region. The three elements, tectum, paries and solum nasi, combine to form the shell-like structure known as the ectethmoid. Laterally the dorsal portion of this is in relation to the orbit.

The nasal septum or mesethmoid (fig. 11) is a vertical and roughly pentagonal plate of cartilage, constituting the ventral end of the central stem of the chondrocranium. The dorsal border is marked above by the interrupted line of attachment of the dorsal surface of the tectum nasi, which separates the surface of the nasal from that of the interorbital septum; below this these surfaces have no definite delimitations. The cranio-dorsal border, after passing over from that of the interorbital septum, runs horizontally forward for a short distance, and then mounts rapidly and evenly to reach the highest point of the chondrocranium in the conspicuous crista galli. The latter marks the

widest part of the septum. The outer edges of this border, except in the upper portion of the crista galli, show short lateral eminences, which project into the fenestra cribrosa. These projections will later coalesce with others from the upper edge of the side-wall, and thus form the dorsal portion of the cribriform plate. In front the crista galli passes over upon the cranio-ventral border, which is straight, and sharply inclined downward, while laterally it is directly continuous throughout with the ventral portion of the tectum nasi. By reason of the fact that the tectum rises somewhat, as it springs from the septum, the upper border of the latter lies here at the bottom of a shallow furrow, the sulcus supraseptalis (fig. 1), which reaches from the crista to the ventral tip of the capsule.

The ventral border of the septum is straight and free, and marks the anterior extremity of the mesethmoid, forming the medial limit of the incisura narina, the representative of the fenestra narina of some of the lower forms. At its lower end it meets the caudal border at an angle of 113°. The caudal border is almost straight, horizontal, and thickened throughout, but much more so dorsally than ventrally, so that it resembles a cone, this similarity being rendered more striking by the fact that the transition to the thin part of the septum above is quite abrupt, thus resulting in the formation, on each side, of a shallow furrow (figs. 14 to 18). Near the ventral extremity the caudal border shows on the right side, but not on the left, a lateral connection with the cartilages of Jacobson (fig. 11), and, in front of this, bilateral unions with the ventro-lateral processes (Fawcett '11), the latter appearing immediately behind the front end. Projecting backward from the posterior of these attachments, lying parallel with and below the caudal border, in a position corresponding to about the middle of its ventral half, may be seen the cartilages of Jacobson, or the anterior paraseptal cartilages (figs. 2 and 18). Behind these the dorsal portion of the border, in its caudo-lateral aspect, is covered by the thin plates of the vomer (fig. 2).

The surfaces of the septum are for the most part smooth, but in the region below the crista galli there is a deflection to the left;

on the right side this appears as a well-marked furrow, running from above downward and forward (fig. 11). In the area just above the anterior paraseptal cartilage the furrow lying above the lower, thickened border is somewhat deepened, and in this hollow is to be found the anlage of the organ of Jacobson (figs. 11 and 18).

An interesting feature of the mesethmoid is found about the middle of its dorsal half (the part corresponding to the future lamina perpendicularis of the ethmoid bone), in the form of two paired, elongated cartilages, very small in size, which lie parallel with, and close to, the surface. These may be termed the *superior paraseptal cartilages* (figs. 11 and 16), and though mature, their cartilage is younger in type than that composing the adjacent septum. The cartilage on the right is somewhat the longer, measuring 13 mm., the left being 11 mm., and in direction the right is parallel with the caudal border of the septum, while the left runs slightly upward, as well as backward. The nasal septum, opposite the anterior part of each cartilage, and for a short distance in front of it, shows a slight swelling, and the anterior part of the paraseptal cartilage lies just lateral to and somewhat below this. So closely does the paraseptal cartilage lie to the nasal septum that it is difficult to make out a separation, but by the aid of the high power and close examination it is seen that the cartilage is separate from the septum, except at two points on the right side, and one on the left. On the right side the connection points are at the anterior extremity, and about the middle, while on the left the sole union is at the anterior end. Thus each cartilage presents a free, posteriorly projecting extremity. From the caudal edges of each cartilage there stretches downward a sheet of young connective tissue. Figure 16 shows the relationships of the superior paraseptal cartilage to this sheet, and it will be seen that, where the cartilage is free from union with the septum, as it is on each side in this figure, the relationship of the cartilage to the membrane is somewhat similar to that of a sesamoid bone to its tendon, for the real upper connection of the membrane appears to be somewhat above the cartilages, where it becomes continuous with the perichondrium

of the septum, as shown in this figure. The two sheets unite below the septum, and in this region, which marks their thickest part, they contain the slender spicules of membrane bone which represent the vomer. Though they are found throughout the extent of the vomer they disappear shortly beyond its extremities.

Fawcett ('11) in his description of the paraseptal cartilages finds a similar sheet of condensed mesenchyme, and gives to it the name "suspensory membrane," stating that it envelops the anterior and posterior paraseptal cartilages, and extends between them; further that in the interval between these cartilages the vomer is developed (following Zuckerkandl '08). I am unable to discover in my model any trace of this "suspensory membrane" in front of the ventral extremity of the vomer, so that it has, obviously, nothing to do in this stage with the support of the anterior paraseptal cartilages; moreover it is not found behind the dorsal extremity of the vomer, and hence cannot function in the suspension of the processus cupularis posterior (posterior paraseptal cartilage of Fawcett) which evidently represents the last rudiment of the posterior transverse lamina of such forms as the rabbit (Voit). Furthermore, since the cellular composition of this membrane is apparently the same as that which forms the membranous anlage of any of the membrane bones, and its situation is that which will be occupied by the future upward-growing vomer, and since the vomer is to be found within its thickened caudal portion, it would appear that it is simply the membranous anlage of the vomer. The term 'suspensory' would seem to be misapplied, since the bony elements enclosed by it cannot be said to be suspended, any more than the early osseous spicules of any other membrane bone may be said to be suspended in their membranous anlagen, and the cartilaginous elements are not enclosed by it; indeed the so-called posterior paraseptal cartilages, as Fawcett himself states, are continuous with the lateral walls of the nasal capsule (fig. 14). Fawcett evidently believes that this membrane once sustained the cartilago paraseptalis communis, of such forms as the rabbit, and that the vomer is a covering bone which surrounds and takes the place of this

cartilage when it disappears, although the vomer is present along with the cartilago paraseptalis communis in the skull of the rabbit (Voit). It appears evident from a study of my slides that the vomer attains its adult condition by advancing upward in this sheet of mesenchyme, and thus comes to enclose the septum. What part, if any, the superior paraseptal cartilages play in the development of the vomer, or indeed what their real significance is, I am unable to say.

At the ventral end of the caudal border of the mesethmoid, and lying almost parallel with it, there are to be seen, upon either side, the small, straight, rod-like ventro-lateral processes (figs. 2, 3 and 18), 9 mm. in length in the model, connected by their ventral extremities with the septum (fig. 11), but having their dorsal ends free, the greater part of their length being separated from the septum by perichondrium. The condensed mesenchyme of the ventral tip of the maxilla appears immediately beneath them (figs. 2 and 18), and their material is cartilage of the same character as that of the adjacent septum. Though their dorsal extremities come into close contact with the cranio-ventral process of the median Jacobsonian cartilage, they are not connected therewith.

The Jacobsonian or anterior paraseptal cartilages (figs. 2, 3 and 18) consist of two paired masses, medial and lateral, found immediately dorsal to the ventro-lateral processes. The medial mass is a quadrangular, inwardly concave plate, 28 mm. long, whose long axis is parallel with the lower border of the mesethmoid, with which its upper edge is in close apposition, being, for the most part, only separated by perichondrium. It is much the larger of the two, and lies at a lower level than the lateral mass. The ventral extremity of the plate is drawn out to a rather sharp free point, known as the *ventral process* (fig. 2), its tip lying just below the septum. The lower border is marked, rather nearer the ventral than the dorsal extremity, by a projection, directed downward, which, however, is terminated by a sharp, backwardly turned point of cartilage, this structure being known as the *caudal process* (figs. 2 and 18). The dorsal termination is very blunt; it may be described as the dorsal bor-

der. The cranial border, almost parallel with the caudal border of the mesethmoid, presents near the ventral process a long, slender limb 1 cm. in length, which curves upward and forward, to come into close contact with the dorsal tip of the ventro-lateral process, and thus to reach the most ventral extremity of this cartilaginous mass. On the left side this off-shoot, which may be known as the *cranio-ventral process* (figs. 2 and 18), is disconnected from the septum, though only separated therefrom by a thin sheet of perichondrium, but on the right side a connection to the septum appears near the ventral end of the process. This connection, however, is very meager, the surrounding perichondrium almost cutting it off, and it would seem to be secondary. The cartilage of which the plate is composed is similar to that of the septum within. The two plates enclose a space, open below, which is filled with dense connective tissue, and at the dorsal border of the cartilages the ventral tips of the vomer are seen in it. The ventral process is connected laterally with the lateral Jacobsonian cartilage by cells of procartilage.

The lateral member of the anterior paraseptal cartilages (figs. 2–3) is a short, curved rod, 1 cm. in length, whose concavity is directed downward, forward and slightly inward, lying almost parallel with the cranio-ventral process of the medial mass which is to be found immediately internal to it. The entire lateral mass is of a younger type of cartilage than that composing the larger Jacobsonian cartilage, and upon examining the sections it is seen that it is connected with the latter at a point near the ventral process by procartilage. Otherwise the lateral mass is quite free. The adjacent portion of the lateral wall is marked by the prominent paraseptal process (fig. 2), whose tip is composed of young cartilage, and between this and the lateral Jacobsonian cartilage there is a zone of loose tissue which suggests an earlier connection between these points such as exists in the rabbit (Voit) in the form of the anterior transverse lamina. The ectethmoid would then be united with the medial Jacobsonian cartilage, the lateral member being probably a rudiment of this lamina.

In the ectethmoid (fig. 12), as we have seen, there may be recognized a roof, or tectum nasi, a lateral wall, or paries nasi, and a floor, or solum nasi. Its only connections are made medially with the septum (figs. 11 and 12) and laterally with the cartilago sphenoethmoidalis (fig. 1), both unions being through the roof. The posterior, or subcerebral portion of the tectum nasi is as yet imperfectly developed, and is concerned principally in the formation of the lateral delimitation of the fenestra cribrosa, the representative of the future cribriform plate. Dorsally this subcerebral portion is wide and flattened, and forms part of the ventral boundary of the fissura orbitonasalis. Medially it is connected with the nasal septum by a short line of attachment, interrupted by small foramina (fig. 12) while laterally it is bounded by the broken line of union with the cartilago sphenoethmoidalis. This portion narrows as it is followed ventrally, and forms the rather uneven lateral boundary of the fenestra cribrosa.

The ventral border of this fenestra is formed by the dorsal edge of the prominentia superior (fig. 1), which is a medial continuation of the sphenoethmoidal commissure connecting this to the nasal septum in front of the crista galli. Projecting backward into the fenestra cribrosa from the point of union of the sphenoethmoidal commissure with the superior prominence is a short spicule of cartilage, known as the *processus cribroethmoidalis* (fig. 1), also present in the model of Hertwig. It forms the median boundary of a small incisure, known as the *incisura cribroethmoidalis* (fig. 1) and appears to be the representative of the foramen cribroethmoidale of the rabbit (Voit), through which the anterior ethmoidal branch of the ophthalmic division of the 5th nerve passes into the nasal from the cranial cavity, to emerge, as we shall see, through the foramen epiphaniale as the external nasal ramus. In the model of Hertwig the incisure is still unclosed dorsally. It represents the ethmoidal fissure of the mature bone.

The ventral, or precerebral, portion of the roof is attached, throughout its entire extent, to the nasal septum (fig. 12). It

is almost straight, in the sagittal plane, there being a slight depression between the superior and the supraconchal (Sakterwulst—Voit) prominences. In the coronal plane the tectum is convex upwards, and, when regarded from above, it is seen to be widened by the afore-mentioned prominences.

The paries nasi may be divided into a smooth dorsal portion, the planum antorbitale (fig. 3), which forms the ventro-medial wall of the orbit, and a ventral portion, which presents a much more uneven surface, the two grading into one another in the region of the lacrimal duct. Mead states that "in the reptiles a line joining the corresponding place (commissura sphenoethmoidalis) with the processus maxillaris posterior would separate the paries nasi from the planum antorbitale. The same is true also of the mammals, although here the planum antorbitale is usually oblique instead of transverse." Upon comparison with such forms as the pig the paries nasi (sensu stricto) of man, comprising the part ventral to this line, is very rudimentary. Dorsally the planum antorbitale terminates in a rather sharp point, and upon examining the inner surface of the ectethmoid it is seen that this tip is turned inward and forward, the cartilage being directly continuous, to form the *processus cupularis posterior* (figs. 12 and 14). The border above this extends upward to the bridge of cartilage joining the dorsal portion of the tectum with the septum; it presents near its cranial extremity a small notch (fig. 12), and below this it is fitted closely to the contour of the septum within, the narrow space between being known as the cupulo-septal fissure (figs. 2 and 14) completely filled with connective tissue. This fissure marks off, upon the septum, the delimitation between its interorbital and nasal portions. The upper portion of the planum antorbitale is in close relationship to the ventral root of the ala orbitalis on account of the very rudimentary condition of the interorbital septum in the mammals. A theory accounting for the shortening of the latter is given by Mead who states: "In the evolution into the nasal capsule of the mammals the posterior part of the capsule of the reptiles has been expanded by the backward rotation of the posterior wall (reptilian planum antorbitale), the pivot being the more solid lateral side."

Below the dorsal extremity of the planum antorbitale is a wide notch, the *dorsal palatine notch* (fig. 12), partly filled by the developing upper portion of the palate bone; below this is a rounded angle, from which the sharply-marked lower border runs forward and outward, with a slight concavity downward, to end, by an upward and inward bend, upon the posterior prominence (fig. 3). When the capsule is looked at from below it is seen that the ventral two-thirds of this lowermost border is concerned with the attachment of the solum nasi (fig. 2). Above, the line of attachment of the sphenoethmoidal cartilage marks off the upper surface of the paries nasi from the tectum, and just beneath this line, and close to the surface of the planum antorbitale, but separated therefrom by connective tissue, there is to be seen a small nodule of cartilage, the cartilago paraethmoidalis (figs. 3 and 16) apparently of the same age as that of the adjacent wall. It is oval in shape and bears no apparent important relationship to the neighboring structures. Within the capsule the superior nasal meatus corresponds to the dorsal area of the planum, while the middle meatus is medial to its anterior portion.

The ventral portion of the paries nasi (fig. 3) (paries nasi *sensu stricto*), is thrown into a number of eminences, between which lie corresponding hollows. In its dorsal area is to be seen the prominentia posterior, a small swelling upon which the posterior maxillary process appears. The prominence does not extend so far laterally as the lower border of the antorbital plane behind and below it; the latter is continued upward and inward, curving over the summit of the prominence to enclose, in the downward concavity thus formed, the posterior maxillary process. The latter is wide and flat, projects ventrally and is cut off in front and above by a sharply marked furrow, being unbounded below and behind (fig. 17). The slender lacrimal bone lies along its upper border, and a short distance lateral and below is an elongated nodule of cartilage, the anlage of the processus paranasalis, which may be known as the cartilago paranasalis. This presents a free ventral extremity and a dorsal extremity closely applied to, but not continuous with, the lower aspect of the posterior prominence. It is separated from the

underlying cartilage by a thin sheet of perichondrium, and between it and the processus maxillaris posterior the anlage of the lacrimal duct may be seen. The lower surface of the prominence is rounded, and thus contrasts sharply with the lower border of the planum antorbitale immediately dorsal to it, which is sharply marked, and projects outward and downward beyond the prominence.

The cranial area of the ventral surface presents a smaller eminence, the prominentia superior (figs. 1, 3 and 12), to whose dorso-lateral edge the sphenoethmoidal commissure is attached and which medially goes over into the septum. It is to be found just ventral to the fenestra cribrosa, and the small foramen epiphaniale (fig. 3) is to be seen piercing its ventro-lateral edge. It represents a small cavity, found in the inner capsular wall. This prominence is separate from a larger one, situated upon the lateral wall, some distance in front and below, which I regard as the structure called by Voit the Sakterwulst in the skull of the rabbit. Between these prominences a shallow furrow may be observed, and this opens below into a prominent pit, delimited by the Sakterwulst, and the superior and posterior prominences. This pit corresponds, I believe, to the sulcus lateralis anterior which Voit describes in the skull of lepus, and it follows that the region dorsal to it must represent the wall of the recessus lateralis. The latter is, however, very rudimentary in man, and the corresponding area of the lateral wall in my model appears to be collapsed, when compared with the condition in the rabbit as shown by Voit's illustrations. The anterior prominence of Voit is not to be seen.

The Sakterwulst (supraconchal prominence) is the most conspicuous of all the prominences in the human ectethmoid at this stage, and presents a sharply-marked summit. Behind the latter may be seen an undulating ridge, which passes successively backward, across the sulcus lateralis anterior, over the ridge of the posterior prominence, to reach the lower border of the planum antorbitale (fig. 3). The Sakterwulst corresponds to the ventral extremity of the middle meatus of the nose; below it is a groove leading downward and backward to an incisure in the lower

border of the ectethmoid, the incisura post-transversalis (figs. 3 and 12), behind the processus paraseptalis, the latter being the representative of the anterior transverse lamina of the rabbit (Voit). The ventral surface of the Sakterwulst slopes downward, forward and inward to the upper part of the incisura narina. Upon the edge of this there is, at this point, a small projection, the representative of the cartilago cupularis of the lower forms (fig. 12).

The ventro-caudal portion of the paries nasi is raised into a slight eminence, and upon the ventral edge of this, which bounds the incisura narina, the processus alaris superior appears (figs. 2 and 12) this being, however, but rudimentary in man when compared with such forms as the rabbit. The most prominent feature of the lower edge is the elongated and slender paraseptal process, which points inward, backward and downward.

The solum nasi is formed mainly by the inferior nasal concha, which appears as the inturned lower edge of the paries nasi, and in part by the rudiments of the laminae transversales anterior and posterior, represented respectively by the processus paraseptalis and the processus cupularis posterior. The dorsal portion of the inferior concha is corrugated, and presents a free posterior edge, which meets its median border at a right angle. This dorsal edge is inwardly continuous with the lower extremity of the middle concha (fig. 12), where it joins the inner aspect of the planum antorbitale; with the latter it forms a notch, lodging the ventral portion of the upper border of the palate bone, and known as the *ventral palatine notch* (figs. 2 and 12). A rounded ridge, directed backward and inward, appears upon the lower surface, and separates two grooves, the medial being the more well-marked. This ridge is represented in the floor of the middle meatus by a wide groove which runs backward and inward to terminate by passing over the dorsal edge of the inferior concha, which thus shows a marked concavity upward.

The ventral portion of the solum is narrow and more sloping than the dorsal, and is also smoother. It terminates ventrally at the post-transverse incisure. The medial border of the inferior concha is thickened except at its extremities, and forms the lateral boundary of the basal fissure (fig. 12).

The medial surface of the ectethmoid is complicated, but is, in a general way, concave. Dorsally may be seen (figs. 12 and 14) the processus cupularis posterior projecting forward freely into the mesenchyme. This is the last remnant of the lamina transversalis posterior which is found in the rabbit (Voit), in which animal it connects ventrally with the paraseptal cartilage, but in my model there is no such connection. This is the only part of the dorsal border which turns inward, and is thus the sole representative of the median part of the cupola posterior, described for many of the lower forms. A portion of the dorsal border, a little below the lower margin of the bridge of cartilage which joins the tectum nasi to the septum is partially cut off by a thin sheet of perichondrium, and it also presents a slight thickening. Its cartilage at the ventro-cranial edge is slightly younger than that found in the adjacent wall. This may be the homologue of one of the ethmoidal conchae of the lower forms (fig. 12). Below the dorsal portion of the tectum is to be seen a small fossa, probably the representative of the sphenoethmoidal recess of the adult condition, and this is bounded below by the anlage of the superior nasal concha (fig. 16). The latter is a small ridge of cartilage which stretches across from the medial surface of the planum antorbitale behind to the attachment of the middle concha with the wall, in front.

Below and behind the superior concha is to be seen the superior meatus of the nose (fig. 12), and it may be noted that this narrows below by reason of the fact that the line of attachment of the middle concha, which forms its lower and anterior boundary, runs from above downward, as well as backward.

The middle nasal concha (figs. 12 and 16) is somewhat larger than the superior, and presents an irregular lower edge which may be followed from a swelling of the lateral wall (which corresponds to the antero-lateral sulcus of the outer surface) backward and downward to terminate at the apex of the ventral palatine notch by running over upon the dorsal edge of the inferior concha. The edge of the middle concha is composed of very young cartilage. The middle concha is perforated, near its upper end, by a small foramen, filled by connective tissue. Its

medial surface, in its ventral and upper portion, looks inward, but as it is followed dorsally it is seen to become directed backward, and also to become much narrower, so that the dorso-caudal extremity even looks slightly outward, being separated from the adjacent medial wall of the planum antorbitale by a perceptible interval, the lower limit of the superior meatus, while its dorsal edge shows a slight prominence projecting backward a short distance before the lower end is reached.

The middle meatus (figs. 12 and 16) is quite capacious—almost cavernous—in appearance. Above, it is roofed in by the overhanging middle concha, and below it is delimited by the shelf-like inferior concha, these two conchae meeting dorsally to bound its dorsal extremity, this latter being a deep recess. Ventrally the deepest portion of the meatus is marked by a furrow, which corresponds to the Sakterwulst on the lateral surface. At approximately the center of the middle meatus, close to the lateral wall, but separated from it by a layer of connective tissue, is a small nodule of very young cartilage, surrounded by a shell of procartilage, the latter connecting the nodule dorsally with the wall of the ectethmoid, which shows a prominence at this point. This nodule, which is known as the *cartilago meatus medii*, is situated at a point of the lateral wall just opposite to the posterior maxillary process of the lateral surface (fig. 17), and is surrounded by loose connective tissue. It occurs on both sides, but what its significance may be is uncertain.

At the root of the paraseptal process there may be seen a small hollow, corresponding to the eminence upon the outer surface. The under surface of the ventral portion of the tectum nasi is smooth, concave, and presents, laterally and above, the foramen epiphaniale, aforementioned (fig. 12).

VISCERAL ARCHES

Only the upper two visceral arches, representing Meckel's cartilage with the auditory ossicles and Reichert's cartilage, are shown in the model.

Meckel's cartilages (figs. 3–4) comprise two irregularly curved rods, each of which passes from the ventro-lateral recess of

the otic region to the site of the future mandibular symphysis, and form by the approximation of their ventral, upturned extremities the apex of an angle, the sides of which enclose the triangular area occupied by the structures composing the floor of the mouth. In cross-section each rod is seen to be of the mature type of cartilage and shows an almost uniform diameter, although the middle of the shaft is characterized by a slight but elongated spindle-shaped thickening, while the ventral upturned extremity is thickened and flattened ventro-dorsally. The dorsal extremity of the shaft, too, just before it becomes continuous with the malleus, shows a short fusiform expansion.

After leaving the ventro-lateral recess of the otic capsule, where it is directly continuous with the malleus, the cartilage proceeds forward, inward and downward, lying quite close to the pars cochlearis of the otic capsule (4 mm. in the model). It then changes its direction, passing almost directly forward, and only slightly downward and inward, thus forming, in the portion below the ala temporalis of the sphenoidal anlage, a wide curve with its concavity directed outward, forward and upward. This direction is maintained until the cartilage reaches a point a short distance in front of its termination, when it turns rather abruptly upward, and its tips become flattened, their medial edges being approximated in the midline, but being separated by a thin sheet of connective tissue, as is usual in homo. Thus a second curve, with its concavity upward and slightly outward, is formed. Upturning, enlargement and flattening of the anterior end is noted by Low first in the 18 mm. stage, and is persistent, the tip becoming later constricted off, and appearing in the 95 mm. stage of Low as a small nodule above the symphysis.

Excepting the small portion made up of the posterior fusiform expansion the shaft is flanked laterally by the covering membrane bone of the mandible, which also overlaps the ventral extremity in the manner shown in the Hertwig model, and which was noted by Low as early as the 18 mm. stage. The terminal upturned portion of the cartilage shows a general enlargement of the cells, and to the lateral surface of this the covering bone is applied very closely—indeed it would appear that this area is encased by a thin plate of perichondral bone. Within this the

cells are still larger and vacuolated, and where it fuses with the mandibular bone there is what appears to be a beginning center of endochondral ossification. Here the ground substance is much more deeply staining, and at one point a bud of osteoblastic tissue appears to be invading the cartilaginous mass. Elsewhere, however, the cartilage and covering bone are separated by a narrow interval, containing connective tissue, and nowhere else in the cartilage are there any indications of ossification.

Just beneath the posterior expansion of the shaft is seen the small, flattened tympanic bone (fig. 2), while medial and above the latter, lying with its long axis parallel to that of the Meckelian cartilage, and immediately applied to it, is the slender goniale. Above and lateral to the posterior extremity of the shaft is to be seen the squamo-temporalis.

Ventrally the mylohyoid muscle is attached to the perichondrium of Meckel's cartilage, but in the middle third its attachment is to the inner table of the mandible and its dorsal prolongation, this connection being established just above the cartilage. Hence it would appear that the mylohyoid ridge of the mature bone indicates the original position of Meckel's cartilage.

By reference to the Hertwig model it is seen that in the interval between the 40 mm. and 80 mm. stages there has been a modification of the curve of the cartilages, the dorsal curvature having been eliminated in the older stage, so that the proximal portion of the cartilage is forced away from the cochlea and the angle at the symphysis considerably widened. It would appear that in the process of development the cartilage grows more rapidly in length than in thickness, and hence with advancing age it becomes progressively more slender. This is brought out clearly when my model is compared with the earlier Low ('09) models on the one hand and with the Hertwig model on the other, the cross-section of the rod in the latter being less when compared with its length than is the case in my model, and much less than that of the earlier Low models.

Evidence of beginning ossification and resorption of the cartilage opposite the interval between the lateral incisor and canine tooth germs is first noted by Low ('09) in the 31 mm.

stage, in the form of enlargement of the cells, while in the same region, in the 36 mm. stage, he mentions ossification of the perichondrium with vacuolization and enlargement of the cells. Again, in the 55 mm. stage, he figures this region of Meckel's cartilage almost surrounded by bone, and undergoing resorption. Hertwig's model shows a complete investment of covering bone in this region. My model is intermediate between the 36 and 55 mm. stages of Low, the cartilage being only half surrounded by bone, and ossification just commencing within.

Of the auditory ossicles all are represented in the model (figs. 2 and 3). The malleus, as has been stated, is directly continuous ventrally with the shaft of Meckel's cartilage. Dorsally it is cut off from the incus by perichondrium, though in the model the two are represented as continuous, a lateral furrow marking the intervening boundary. The head of the malleus is large and rounded, and lies just lateral to the tegmen tympani, being separated by connective tissue; its manubrium is long, thickened proximally, and its tip is closely applied to the promontory of the cochlea, a condition which is strikingly different from that found in the model of Hertwig, where there is a considerable interval between these parts, caused apparently by the expansion of the middle ear region, which has thrust the upper end of Meckel's cartilage, with its affixed structures, outward. In the angle between the manubrium and Meckel's cartilage the tympanic and goniale are seen. The goniale, which represents the future anterior process, is at present unattached to the malleus, and remains so till the end of the fifth month (Broman '99).

The incus is completely separated from the malleus, in front, and from the otic capsule, behind, by perichondrium, and presents a body to which is attached a long and a short limb, morphologically resembling the adult condition. The incudostapedial articulation is formed of condensed mesenchyme, and marks the apex of a right angle, open upward, outward and backward, formed by the long limb of the incus and the two limbs of the stapes, and in this angle the facial nerve is to be found.

The stapes at this stage is circular in form, the base being imperfectly developed. The limbs are represented by well-defined, round cartilaginous rods.

Reichert's cartilages (figs. 2 and 4) are the paired cartilaginous rods, lying below the posterior half of Meckel's cartilage, which form the posterior part of the hyoid arch. Each is roughly the shape of a walking cane with a curved handle and a somewhat bent shaft. The handle-like portion is found between the lower end of the crista parotica and the lateral extremity of the jugular foramen, the fenestra perilymphatica being above it, and the paracondyloid process below. It lies quite free in the mesenchyme, separated by that tissue from the otic capsule, a condition agreeing with that described by Jacoby for an earlier stage, in which the cartilages were in contact with the otic capsule, but not fused with it, as they are shown to be in the Hertwig model of a later stage. Each cartilage is of almost uniform diameter throughout, and its direction is from behind forward, inward and slightly downward, the shaft presenting a slight outward and downward bowing, where it sweeps around the promontory of the cochlea, and a gradual inturning toward the distal extremity. As it passes forward the shaft gradually separates from the promontory, to which it is closely approximated, without being actually in contact, and at the same time draws closer to Meckel's cartilage. The terminal anterior tip lies just medial to the angle of the mandible (fig. 2), and above the greater cornu of the hyoid cartilage, which it overlaps for a short distance, without actually becoming contiguous, and it shows a rather younger type of cartilage than the rest of the shaft. The latter differs from that of the chondrocranium in being more reddish in stain.

MEMBRANE BONES

All of the purely membrane bones of the skull are represented in my embryo, though they are as yet but imperfectly developed. The interparietal appears, as has been noted, just lateral to the dorsal occipital prominence as a faintly staining spicule of osseous matter, but owing to the lack of the dorsal sections the extent of the bone could not be ascertained, and hence it was not shown in the model. Though this bone does not appear in the model of Hertwig it must have been present, as this embryo was con-

siderably older than mine. According to Mall ('06) the centers for the interparietal (one on each side) appear on the 57th day and unite on the 58th day.

Situated some distance above the otic capsule, and forming a part of the side wall of the cranial cavity, is the network of bone which is the anlage of the future parietal (fig. 4). It is roughly of diamond shape, with the long axis directed cranio-caudally, and medial to its lower border is the disappearing parietal plate, the two layers, cartilage and bone, being separated by a slight interval filled with connective tissue. There is a considerable area separating this bone from the frontal, and it is also widely separated from the interparietal, there being a very large area at the back of the cranium, behind the parietals and above the tectum posterius, uncovered by bone or cartilage.

The parietal bone is not so dense as the frontal, showing that it is probably later in appearing. Its structure presents no definite center, it being a fine reticulum throughout, though, for technical reasons, it has been represented in the illustrations as a solid plate.

The frontal bone (fig. 4) is similar in structure to the parietal, and encloses the lateral and ventral parts of the anterior cranial fossa. In it two main parts may be distinguished, a vertical portion, convex antero-laterally, and a horizontal portion, which is slightly arched upwards for the accommodation of the structures of the orbit; these being the anlagen of the corresponding parts of the adult bone. Joining these portions is a well-marked, rounded ridge, the representative of the future supraorbital ridge, and here the bone is most densely deposited, especially in the central part of its extent, indicating, probably, that in this position the first masses of osseous tissue were laid down, and not in the region where the frontal eminences will later appear, as is stated in the textbooks. The entire margin of the bone, as well as the greater area of the posterior half, is but a tessellated plate composed of intercrossing osseous spicules. The anterior extremity is rounded, and shows no definite resemblance to the mature condition; it is separated by a considerable interval

from the nasal bone, and almost touches its neighbor of the opposite side, this being the part of the bone which most nearly reaches the median plane. Posteriorly it gradually recedes from this plane, the entire medial edge of the horizontal portion underlying the outward-slanting ventro-lateral edge of the sphenoethmoidal cartilage. Its dorsal extremity is separated by a considerable interval from the parietal bone. It also, for technical reasons, is figured as a plate.

The squamosal (figs. 2, 4 and 13) is a somewhat fan-shaped bone, in which two distinct portions may be recognized; a posterior flattened plate, covering laterally the auditory ossicles and the upper part of Meckel's cartilage, and a ventral, elongated spicule of bone, the zygomatic process, whose tip is found just above the dorsal tip of the zygomatic bone. The upper edge of the flattened portion is convex upward, and is somewhat serrated, the lower border being slightly concave, and passing directly into the zygomatic process. The latter, owing to its lying parallel with the sagittal plane, meets the flattened portion at an angle, as the latter looks outward and forward (fig. 2).

The zygomatic bone (figs. 2 and 4) is somewhat quadrilateral in shape, and thus bears a resemblance to its adult condition. It already shows a body, with four angles, three of which terminate in marked projections. The body is flattened and thin, and the ventral part of its medial surface is in close apposition, though not in union, with the zygomatic process of the maxilla. From the dorso-caudal angle there projects backward a spicule of bone, whose dorsal extremity underlies the ventral extremity of the zygomatic process of the squamosal, thus identifying it with the zygomatic process of the zygomatic bone; the zygomatic arch is, accordingly, incomplete. From the cranial angle there projects upward and slightly backward the rather blunt, but strongly marked, frontal process, lying somewhat ventro-lateral to the upper extremity of the ala temporalis, and a slender elongated and inwardly curved infra-orbital process overlies the outer border of the zygomatic process of the maxilla. The caudo-ventral angle of the body is well-marked, and represents the anlage of the future malar tubercle.

The lacrimal (figs. 4 and 17) is a slender spicule of membrane bone lying along the upper and lateral part of the cartilaginous posterior maxillary process, its long axis being directed from behind forward, inward and slightly upward. Its middle part presents a slight thickening, and the naso-lacrimal duct lies immediately lateral to it.

The nasal bone (figs. 1 and 4) is represented in the model as a thin plate, rounded in outline, flattened, and about 1 cm. in diameter, lying upon the part of the upper surface of the tectum nasi which represents the medial surface of the supraconchal prominence. Behind this plate, and lying close to it, are several minute nodules of membrane bone, which also contribute to the formation of the adult bone. The nasal anlagen lies in a mass of dense mesenchyme, which overlies the entire nasal capsule, similarly to the formation described by Fawcett ('10 a and '10 b) in a 30 mm. human embryo.

The tympanic (figs. 2 and 4) is a short, flat plate of membrane bone, lying beneath the posterior extremity of Meckel's cartilage, and in front of the malleus. Its anterior part is slightly wider than the posterior, and its long axis lies parallel with that of the cartilage, its flattened surface being applied to the latter. The bone is found in an isolated anlage of condensed osteogenic mesenchyme, and is placed lateral to and below the goniale. When compared with the Hertwig model it is seen that the only part which is as yet laid down is the anterior widened extremity, there being no evidence of the ring-like form of the later bone.

By the subsequent outward swinging of the ossicles and attached Meckelian cartilages consequent upon the expansion of the region of the middle ear the plane bordering upon Meckel's and Reichert's cartilages is changed in direction, so that its outer surface looks almost directly downward, as shown in the model of Hertwig, instead of outward, as is the case in my model, and at the same time the interval between these two cartilages is relatively narrowed. This interval the tympanic bone comes to occupy, its dorsal half, as yet undeveloped in my embryo, being applied to the cartilage of Reichert in the Hertwig model, the long process of the malleus occupying a position within the ring.

The goniale (figs. 1-2) is a short, somewhat flattened, rod of membrane bone, lying immediately below and medial to the posterior fusiform enlargement of Meckel's cartilage, and so close to the latter that it appears to be developed from the perichondrium covering its surface. Its long axis is parallel with that of Meckel's cartilage, and its anlage is quite separate from that of the tympanic, which lies on a lateral and caudal plane. Its posterior end approaches close to the neck of the malleus, but does not actually become continuous therewith until the end of the fifth month (Broman '99), when it becomes the anterior or Folian process of that ossicle, a fact which was demonstrated by Dreyfuss ('93). Gaupp ('05 and '11) has given strong reasons for the identification of the processus Folianus with the goniale of the reptiles, and it is on his authority that I have used that name for it here. The bone is shown in the Hertwig model, and also appears in Low's illustration from a 95 mm. human embryo under the name of 'processus folianus.'

The vomer (figs. 2, 16, 17 and 18) is represented by two slender strips of bone lying one on either side, immediately caudo-lateral to the lower border of the mesethmoid, the two almost enclosing this border excepting for a narrow strip between their lower edges. The dorsal extremity of each strip is blunt, but the ventral is drawn out to a fine point, and near the latter there is a bridge between the two bones. The ventral point projects only a short distance in front of the dorsal border of the larger Jacobsonian cartilage.

The maxilla (figs. 2, 4, 16 and 17) is an irregular mass of cancellous bone which lies in a notch on the ventro-lateral aspect of the ectethmoid, and it already shows the frontal, alveolar, palatal and zygomatic processes. The central mass of the bone is irregularly triangular in form upon coronal section (fig. 17), the longest side of the triangle being applied to the ethmoidal cartilage, while the medial angle represents the palatal process, the upper angle the frontal process, and the remaining angle, which is a right angle, the alveolar process. The pointed, upwardly-directed frontal process reaches a level somewhat above

that of the lacrimal; its posterior surface forms the anterior wall of the space containing the naso-lacrimal duct (fig. 4). The palatal process does not quite reach to the median plane and anteriorly it is separated by a notch from the extremity of the alveolar process: its medial border is below and lateral to the vomer, and its posterior border underlies the palatine bone for a considerable distance.

The alveolar process is a very irregular ridge of bone, occupying the inferior and lateral edge of the maxilla, and its anterior end extends medially almost to the mid-line, coming to lie in advance of the palatine process. In its lower aspect may be seen the depressions for the future dental alveoli. The zygomatic process is a more lateral coarse spicule of bone, which projects backward and outward until its extremity almost touches the inner surface of the zygomatic bone. It is perforated from above downwards by foramina, and just before it joins the body of the bone it sends up a small process, which marks off a groove occupied by the second branch of the trigeminal nerve (fig. 17). There is as yet, therefore, no foramen for this nerve trunk. The posterior edge of this process is continuous inwardly with the posterior edge of the palatal process. Anteriorly a spicule from the upper part of the anterior extremity of the alveolar process projects forwards, and lies lateral to and below the anterior part of the anterior paraseptal cartilage, to which it is closely applied. This is the anlage of the anterior nasal spine.

The palate bone (figs. 2, 3, 14, 15 and 16) is a thin, delicate lamella of osseous tissue, strongly concave inward, which walls in the dorsal portion of the nasal cavity. Its borders are serrated; the upper being fitted into the dorsal palatine notch of the ectethmoid, and ventrally to this into the ventral palatine notch. The incurled lower edge (fig. 2) which becomes the palatal plate, approaches but does not meet its fellow of the opposite side, being separated from it in the model by a space of 15 mm. Dorsally the anlage of the pyramidal process is represented by a thickened and irregular projection which lies ventral to the medial pterygoid lamina.

The medial pterygoid plate (figs. 2, 3 and 10) is represented by an elongated and somewhat spiral rod, lying behind the palate bone and medial to the lateral portion of the ala temporalis. Two distinct portions may be recognized in it, the upper part being osseous and the lower cartilaginous. The former is bent dorsally and from its most posterior extremity, which is about 3 mm. from the medial angle of the lateral portion of the ala temporalis, a short but stout process projects cranio-medially, marking the highest part of the rod. Below it terminates in the cartilaginous hamular process, which points almost straight downward.

The membrane bone of the upper portion is typical in structure, and when followed downward shows a gradual transition into the cartilage of the hamular process. The cells of the membrane bone enlarge, their capsules swell, and at the same time the ground substance becomes lighter in color. Nearer the cartilage which forms a cap to the extremity of the osseous rod the capsules become smaller, the ground substance increased in amount, and the line of transition is not sharply marked. Though the tip of the cartilage partakes of many of the properties of normal cartilage—staining lightly, having a homogeneous matrix, the nuclei surrounded by capsules, and the whole being enveloped by a closely-fitting, sharply defined, thin sheet of perichondrium —yet there are several points of difference which mark out this mass of cartilage as different from that found elsewhere in the primitive skull. The matrix stains slightly more darkly, the nuclei are larger and lighter in color, and the capsules surrounding them are relatively smaller, when compared with the size of the nuclei. Altogether the cells resemble those of membrane bone more than they do those of typical cartilage.

The mandible (figs. 3–4) is a plate of membrane bone lying immediately lateral to Meckel's cartilage, and separated from this throughout its extent by connective tissue, except in a small area in the region of the lateral incisor and canine tooth germs, where, as has been noted, the bone is directly applied to the cartilage, appearing like ossified perichondrium. The posterior part of the bone is wider than the anterior, and is marked

cranially by a distinct indentation, the representative of the future sigmoid notch, which separates the anlagen of the condylar and coronoid processes. Just external to the latter is the zygomatic bone, and internal to it is the cartilaginous pars temporalis of the sphenoid. The lateral surface of the plate shows, about the junction of the anterior and middle thirds, a distinct opening, the mental foramen, and at this point there is a bend in the bone, the direction of the long axis changing from downward and forward to upward, inward and forward. A short distance above the lower border of the bone, and parallel with it, a groove may be seen upon the lateral surface, more distinct posteriorly than anteriorly. This is also shown in the illustrations of Low's older specimens, and appears to represent the line of insertion of the masseter.

The anterior half of the bone shows an inner table, regarded by some authors as the splenial element, which separates the vessels and nerves from Meckel's cartilage, becoming continuous anteriorly with the ossified perichondrium immediately surrounding the cartilage. About the center of the long axis of the bone the so-called splenial element dwindles in height, and terminates as a thin, backwardly projecting spindle of bone, to which the mylohyoid muscle is attached. Anteriorly the membrane bone overlaps the termination of the cartilage of Meckel, and thus shows the condition observed by Low as early as the 18 mm. stage.

On the whole, the shape of the mandible suggests the adult condition, though it is considerably more slender, and the angle is more obtuse. Immediately caudo-medial to the latter is the tip of Reichert's cartilage. There are no accessory cartilaginous nuclei observable, as Low describes in an older model.

Low ('05) has held that each half of the mandible is laid down as a single skeletal element, the dentary, the so-called splenial element being simply an extension of this. The condition in my embryo supports this finding, the main portion of the bone being formed of the dentary, the splenial element being but a thin lamella of osseous tissue, directly continuous below with the

anterior portion of the dentary, and posteriorly terminating in a slender process, as described. Within this medial plate the tooth gutter is well-marked. The condition is very similar to that shown by Low ('09) in his text figure 4.

CONCLUSION

From the foregoing brief account of the morphology of the human fetal skull of 40 mm. it will be seen that it presents, at this stage, several unique features. The structure of the parts surrounding the foramen magnum is significant in casting, perhaps, some further light upon the genesis of this interesting region. The presence of a fairly clearly defined neural arch of the occipital vertebra has been dwelt upon, and its interpretation discussed. The finding of a small nodule of cartilage above and in front of the cochlea is, so far as I am aware, a contribution to our knowledge of the parts in this area. Other new features are the cartilagines paraethmoidalis, meatus medii and paraseptalis superior, all of which have been briefly described; in addition may be mentioned the lateral and dorsal cranial cartilages, and the paranasal cartilage, lying lateral to the lacrimal duct.

Finally, I wish to express to Professor McMurrich my sincere appreciation of his kindness in placing at my disposal the material for this research, and the freedom of the Anatomical Laboratory of the University of Toronto, as well as of his abundant advice and encouragement.

Anatomical Laboratory, University of Toronto
September, 1913

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